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Global Analysis of Proteins Synthesized during Phosphorus Restriction in *Escherichia coli*

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The pattern of proteins synthesized in *Escherichia coli* during steady-state growth in media with ample inorganic phosphate (P_i), upon limitation for P_i (without an alternative phosphorous compound), and during steady-state growth in media containing phosphonate (PHN) as the sole P source was examined by two-dimensional gel electrophoresis. Of 816 proteins monitored in these experiments, all those with differential synthesis rates greater than 2.0 or less than 0.5 upon phosphate limitation (P limitation) or during growth on PHN compared with their rates in the cultures with P_i were classified as belonging to the PL or PHN stimulon, respectively. The PL stimulon included 413 proteins, 208 showing induced synthesis and 205 showing repressed synthesis. The PHN stimulon was smaller: it included 257 proteins; 227 showed induced synthesis and 30 showed repressed synthesis. The overlap of the two stimulons included 137 proteins: most (118) were ones showing induced synthesis. The promoter regions of genes for several of the proteins with induced or repressed synthesis contained sequences which resembled the consensus sequence for PhoB binding. The aggregate mass of proteins responding to P limitation or growth on PHN was 30 to 40% of the cells' total mass. By comparing the proteins responding to P limitation with those responding to growth on PHN, one can speculate which proteins are likely involved in adapting cells to new P sources or in preparing cells to survive stationary phase.

Microorganisms have evolved mechanisms to acclimate rapidly to changes in their environment. Three of the more common strategies are (i) adapting to different nutrient supplies through the induction or activation of enzymes required to utilize these nutrients (29) (adaptive response), (ii) producing toxins or antibiotics which kill other cells (21) or invading other cells in the environment (24) (pathogenic response), and (iii) switching to a stationary mode of growth, which brings about resistance to many stresses and the ability to survive long periods without nutrients (38) (survival response).

For *Escherichia coli*, inorganic phosphate (P_i) is the preferred phosphorus (P) source. When P_i is not available, *E. coli* is known to activate an adaptive response, which includes about 50 proteins involved in scavenging other forms of phosphates (such as organic phosphates) or in utilizing other P sources (44, 52). Phosphonates are one of the alternative P sources that *E. coli* can use. These molecules, which have carbon-phosphate bonds, are abundant in nature, particularly in eukaryotic membranes (e.g., in *Tetrahymena* species [13]). The antibiotic fosfomycin, made by *Streptomyces* species, is a phosphonate (4). The genes that encode proteins involved in the uptake and cleavage of phosphonate in *E. coli* lie in an operon, *phnCDEFGHIJKLMNOP* (53, 55). Many of the genes encoding proteins that are part of the adaptive response are members of a single regulatory network (the PHO regulon) defined by the involvement of a two-component regulatory system, PhoR and PhoB (20, 23, 44, 51, 52).

In addition to the adaptive response stimulated by P_i depletion, *E. coli* also appears to induce a pathogenic response (39) and a survival response (42). *E. coli* can survive for at least 7 days without a P source (42). Most of the proteins known to be part of the adaptive response (such as alkaline phosphatase and the membrane porin, PhoE) are induced by P depletion but not by depletion of other nutrients. Some of the other proteins induced by this starvation (but with unknown functions) are also induced by starvations of other nutrients (e.g., carbon, nitrogen, and sulfate) (9, 38, 54), suggesting that some aspects of the pathogenic and/or survival responses induced by P starvation may be similar to those brought about by depletion of other nutrients (22, 38, 56).

E. coli is estimated to encode about 4,000 proteins. Fewer than half of these have been associated with a function or have been identified as being induced by some environmental stimulus. The function of, or requirement for, the other 2,000 or so proteins remains a mystery. Many of these are probably part of adaptive, pathogenic, and survival responses that have not been detected by reductionist techniques or are present only under conditions which are not easily mimicked under laboratory conditions. Over the past 20 years, many techniques that allow more global analysis of the genes (or gene products) turned on and off by different conditions have been developed (29).

A global examination of the response of cells to P_i starvation has been done at the transcriptional level (3). Radiolabeled cDNA made from RNA isolated from a phosphate-starved culture was used to probe blots of 476 clones carrying different regions of the *E. coli* chromosome. Nineteen of the clones appeared to contain genes transcribed at higher levels during P_i starvation.

Another global analysis is the *E. coli* gene-protein database (34, 46). The goal of this database is to catalog when and to what level each protein-encoding gene is expressed. Two approaches involving the use of two-dimensional (2-D) polyacrylamide gel electrophoresis (32) are being employed in this global analysis. The first, called the genome expression map, is designed to link the product of each protein-encoding gene to

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TABLE 1. Assessment of reproducibility of data from duplicate gels and samples

Expt set[a]	Expt gel[b]	No. of spots[c]	Median distribution ratio[d]	Percentile[e]			
				25	75	12.5	87.5
PW	1a	824	1.43	0.83	1.74	0.68	2.32
	1b	769	1.12	0.97	1.32	0.83	1.83
	2a	792	0.91	0.76	1.12	0.61	1.38
	2b	810	0.88	0.61	1.38	0.47	1.24
PLE	1a	790	1.21	1.04	1.48	0.90	2.11
	1b	748	0.88	0.71	1.05	0.56	1.23
	2a	838	0.98	0.84	1.13	0.70	1.39
	2b	742	0.97	0.78	1.24	0.61	1.59
PLL	1a	853	1.43	1.21	1.76	0.99	2.33
	1b	818	1.21	1.02	1.45	0.83	1.82
	2a	744	0.58	0.51	0.70	0.40	0.86
	2b	733	0.91	0.78	1.67	0.63	1.30
PE	1a	715	1.14	0.98	1.31	0.78	1.47
	1b	696	1.13	0.97	1.33	0.93	1.52
	2a	731	0.65	0.54	0.80	0.43	1.00
	2b	701	1.00	0.83	1.20	0.71	1.41
PHN	1a	682	1.26	1.00	1.45	0.88	1.66
	1b	802	1.05	0.87	1.27	0.71	1.48
	2a	733	0.84	0.66	1.01	0.52	1.20
	2b	585	0.78	0.58	1.03	0.38	1.11

[a] Each experiment set is a series of four gels consisting of duplicate gels for two samples (see Materials and Methods). In this table and all other tables and figures, the value for an individual protein is the mean of the values obtained from the four gels.
[b] 1 and 2, samples of different cultures; a and b, different gels of the same sample.
[c] The number of protein spots detected and quantitated.
[d] For each protein on the gel a ratio of the ppm value from that gel to the mean ppm for that protein from the four gels was calculated. The median for the distribution of these ratios was calculated.
[e] The variance in the data with respect to the median. The median is the middle value for all numbers in the distribution. By definition, half of the datum points are included between the 25 and 75 percentiles and 75% of the points are included between the 12.5 and 87.5 percentiles.

a position on the 2-D gels (37). The second project, called the response-regulation map, is focused on cataloging the conditions under which each gene is expressed and on determining what molecules regulate their expression (46).

The response to P_i depletion has been qualitatively examined on 2-D gels for *E. coli* (9, 46). In one of these studies, about 80 proteins were observed to be induced (46). Thirteen proteins induced by P_i starvation were also induced by nitrogen and carbon starvation (9). Those proteins synthesized in increased amounts in response to multiple nutrient starvations are likely to be involved in survival responses. Similar comparisons (also with 2-D gels) have been done for *Salmonella typhimurium* (41), a *Vibrio* sp. (31), and *Bacillus subtilis* (11).

TABLE 2. Summary of SE between different samples and different gels

Expt	No. of proteins in set of gels[a]	No. of proteins with SE of:	
		≤20% of mean	>20% to ≤50% of mean
PW	806	684	122
PLE	759	668	91
PLL	748	340	408
PE	835	565	270
PHN	846	525	321

[a] The number of protein spots quantitated.

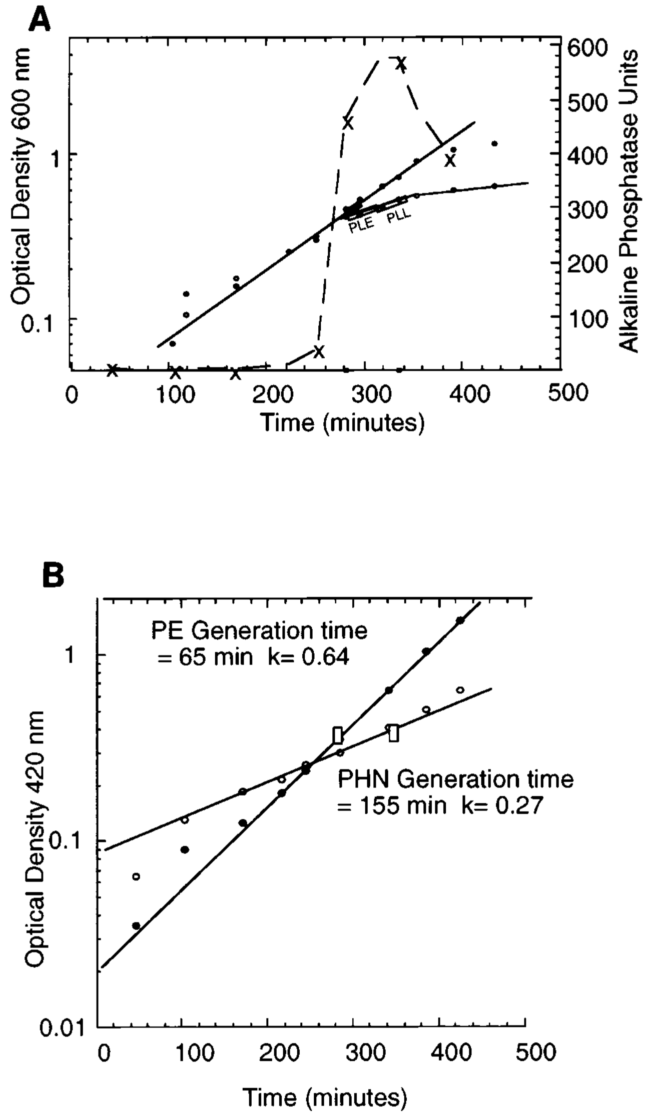

FIG. 1. Growth with different phosphorus sources. (A) Growth of strain W3110 in media with ample P_i (●) and limiting P_i (○). The units of alkaline phosphatase (×) were determined from samples of a culture growing in medium containing limiting P_i. (B) Growth of strain EP820 in glucose minimal MOPS media containing ample P_i (●) and PHN (○).

The global quantitative studies presented in this paper were designed in part to tally proteins involved in the adaptive and survival responses resulting from P restriction. Two P-restrictive conditions were chosen: (i) growth in media containing a limited amount of P_i which causes cell growth to cease as the P_i is depleted and (ii) growth in media containing phosphonate as the only P source. Three compendiums are reported: (i) the identification of the stimulons for each of the two growth conditions, (ii) comparison of the two stimulons to reveal shared and unique protein responders, and (iii) an examination of the magnitude of the switch in gene expression in the two responses with respect to the cell's translational capacity. By employing the *E. coli* gene-protein database (46), 88 of the responding proteins were identified.

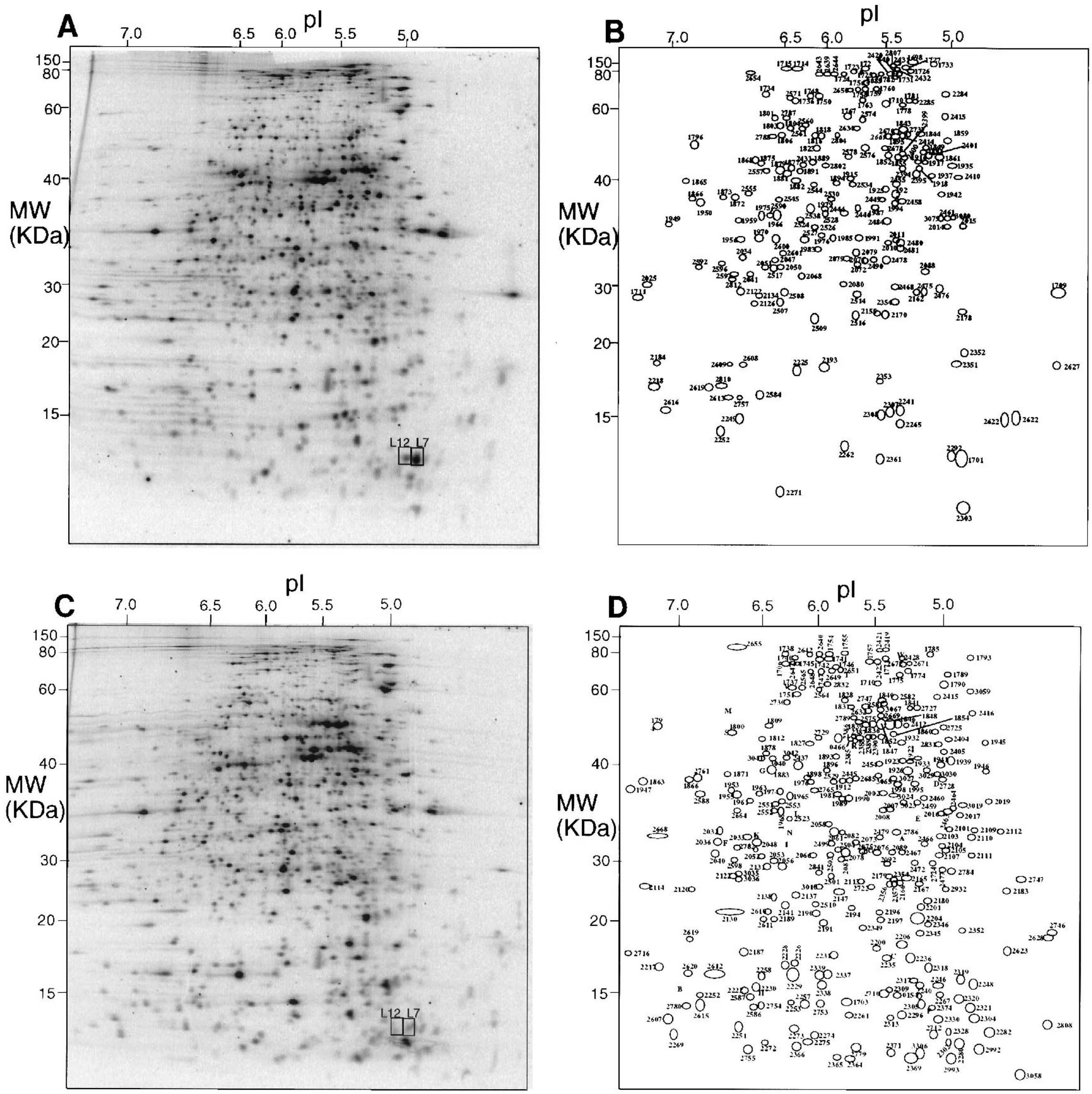

FIG. 2. 2-D gel patterns of proteins synthesized during growth with excess P_i (PW) (A), during P limitation (PLE) (C), and during growth on PHN (E). In order to display the locations of the numerous proteins with repressed (B) or induced (D) synthesis during growth on PHN and/or P limitation compared with their synthesis in excess P_i conditions, two synthetic images were created. The numbers in panels B and D refer to the protein's RRM name, found in the first column in Table 3. The boldfaced letters in panel D indicate the estimated locations of the products of genes previously determined to be induced by phosphate starvation by various methods (except 2-D gel electrophoresis): A, *phnB*; B, *phnG*; C, *phnH*; D, *phnI*; E, *phnJ*; F, *phnK*; G, *phnM*; H, *phnO*; I, *phnP*; J, *phoB*; K, *pstB*; L, *pstC*; M, *ugpB*; N, *ugpE*; O, *ugpQ*; P, *phnA*; Q, *phnB*; R, *agp*; S, *appA*; T, *cpdB*; U, *gltF*; V, *oppA*; and W, *pepN*.

MATERIALS AND METHODS

Strains and media. *E. coli* W3110 was used for the experiment comparing excess P_i media with P_i-limited media. For the experiment comparing growth in excess P_i media with phosphonate-containing media, a derivative (strain EP820) of W3110 that could utilize phosphonate as a sole P source was used (51). Strain EP820 was constructed by P1-mediated transduction (25). The donor for the transduction was strain BW15268 (16). Colonies able to grow on phosphonate (Phn^+) were selected on morpholinepropanesulfonic acid (MOPS)-glucose agar plates containing 0.0132 mM potassium monophosphate and 0.08 mM 2-aminoethylphosphonate (PHN) (Sigma Chemical Co.).

MOPS minimal media were prepared as previously described (27). All media contained 0.01 mM thiamine. Media with different compositions were prepared as follows: medium 1, 0.4% glucose–1.32 mM K_2HPO_4 for medium with ample phosphate; medium 2, 0.4% glucose–0.066 mM K_2HPO_4 for P_i-limited medium; medium 3, 0.04% glucose–1.32 mM K_2HPO_4 for glucose-limited medium; medium 4, 0.4% glucose–0.08 mM PHN for phosphonate medium; and medium 5, 0.4% glucose–0.0132 mM K_2HPO_4–0.08 mM PHN.

Growth and radioactive labeling of cultures. Cultures were grown overnight at 37°C in medium 3 (for W3110 and EP820) and medium 5 (for EP820). The overnight cultures were diluted 1:20 into medium 1 (for W3110 and EP820),

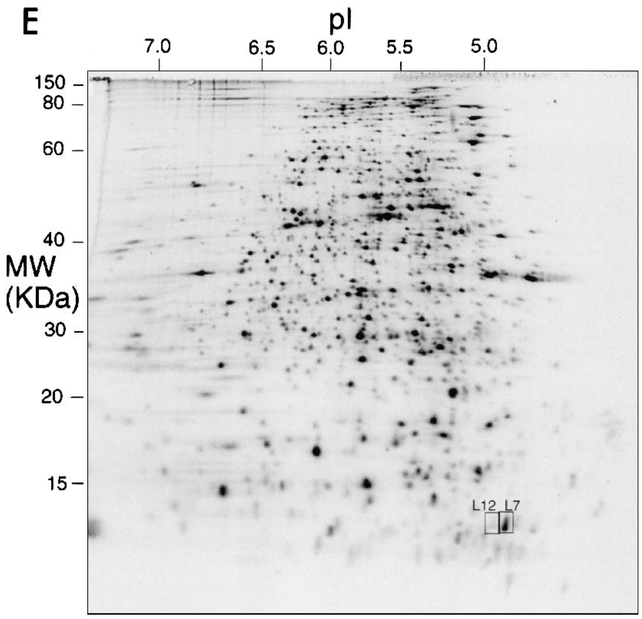

FIG. 2—*Continued.*

medium 2 (for W3110), and medium 4 (for EP820) and incubated at 37°C. At the appropriate times (as described below), a portion (1 ml) of each culture was labeled with [^{35}S]methionine (593 Ci/mmol; 0.1 mCi/ml) and then chased for 2 min with 0.167 ml of 0.2 M methionine. Steady-state cultures of W3110 grown in medium with ample P_i (medium 1) were labeled for 8 min, starting when the cultures had reached an optical density at 600 nm (OD_{600}) of 0.35, the OD at which the culture with limited P_i changed its rate of growth. Within 8 min, the culture should incorporate most of the radiolabel. These samples are designated PW for ample phosphate W3110. The cultures of W3110 grown in P_i-limited medium (medium 2) were labeled from 10 to 30 (early) and from 30 to 60 min (late) after an inflection in the growth curve was observed at OD_{600} of approximately 0.35 (see Fig. 1A). The net synthesis of individual proteins during these non-steady-state growth periods will be revealed by these pulses. The P_i-limited culture was growing at a very low rate for both pulse-labels. These cultures were designated PLE for phosphate limitation early and PLL for phosphate limitation late. Steady-state cultures of strain EP820 grown in ample phosphate and phosphonate media (media 1 and 4) were labeled for 10 min at OD_{420} of 0.45. Although the growth rates for these two cultures were very different, the protein chain elongation rate should be the same because the incubation temperature was the same. The EP820 samples are designated PE and PHN for ample phosphate EP820 and phosphonate, respectively. Protein extracts were prepared as previously described (49). A portion (3 μl) of the cell extract was precipitated with 5% trichloroacetic acid containing methionine (3 g/liter) to determine the amount of radiolabel incorporated into the protein.

Alkaline phosphatase assays. Alkaline phosphatase levels were determined by a slight variation of the permeabilized whole-cell assay previously described (10). A portion of the culture was diluted 1:10 into reaction buffer (1 M Tris-HCl [pH 8.0] at 25°C), permeabilized by the addition of hexadecyl trimethylammonium bromide (CTAB) (to a final concentration of 0.005%), and vortexed for 5 to 10 s. The reactions were carried out at 22°C, initiated by the addition of *para*-nitrophenol phosphate (final concentration, 0.04%), and stopped with KH_2PO_4 (final concentration, 0.1 M). The number of alkaline phosphatase units was calculated by $10^4 \times [OD_{420} - 1.75\ OD_{550}]/[\text{time} \times OD_{600}]$, where OD_{420} and OD_{520} are the absorbances of the reaction mixture at 420 and 520 nm, respectively (path length, 1 cm); OD_{600} is the absorbance of the original culture (prior to the 10-fold dilution) at 600 nm (path length, 1 cm); and time is the duration (in minutes) of the reaction.

2-D gels and analysis. 2-D polyacrylamide gel electrophoresis was performed with the Investigator System (Millipore Corp.) (47). Ampholines at pH 4 to 8 were used for the first dimension, and 11.5% Duracryl (Millipore Corp.) and Trizma pre-set (pH 8.8) (Sigma Chemical Co.) were used for the second dimension. Each gel was loaded with 10^6 cpm of the radioactive sample. Each protein extract was run in duplicate. The dried gels were exposed to a PhosphorImager screen for 2 days, and protein spots containing radioactivity were detected with a PhosphorImager (Molecular Dynamics, Inc.) (33). The image was transferred as a 16-bit image file into the Visage software (BioImage, Inc.) where it was converted into an 8-bit image. The Visage software was used to automate the process of finding protein spots within the image, quantifying the density of the spot, converting the density to counts per minute (with a radioactive calibration wedge as previously described [8]), and matching protein spots among the different images. The data from an entire gel were downloaded and merged into a spreadsheet (Microsoft Excel) on a Macintosh computer. Graphing and statistical analysis of the data were done with either Microsoft Excel or JMP (SAS Institute, Inc.).

Data analysis. The total amount of radioactivity (counts per minute) recovered from each gel varied but was usually around 75%. The unrecovered radioactivity should primarily be that of basic proteins which were not resolved by these gels or proteins that did not enter the gel system. No correction was made for unrecovered radioactivity.

For each protein, the amounts of radioactivity (in counts per minute) from four gels (duplicate gels from duplicate experiments) were used to calculate a mean and standard error (SE). When the value for a protein in one gel was significantly different from those in the other three, the outlying value was not used in the calculation of the mean and SE. Because radioactivity at 10^6 cpm was loaded onto each gel, the counts per minute value for each protein hereafter is referred to as parts per million (ppm).

Statistical analysis. Statistical analyses were carried out to assess the quality of the data from each gel. For each gel, a distribution of the ppm values divided by the mean ppm value was generated for each protein on that gel. Accordingly, in the idealized case, the ppm values are identical for the four gels. In such a case, the ratio of the ppm value to the mean ppm value would be 1.0. In an actual experiment, the ppm values for a protein vary among the four gels. Hence, the ppm:mean ppm ratio for a given protein on a gel would be larger or smaller than 1.0. Table 1 summarizes these distributions. The median and the range of the percentiles are an indicator of how the data for each gel fit compared with the data for other three gels. For example, the median (1.12) for gel 1b for the PW experiment set was above 1.0, but 50% of the ratios for that gel fell within a range of 0.35 of the median. The median (0.91) for gel 2a of the same experimental set was skewed below 1.0, but again most of the ratios fell within a narrow range.

To evaluate the variation in the ppm value for each protein, the SE was expressed as a percentage of the mean ppm value. For all experiments except PLL, a majority of the proteins had SEs within 20% of the means (Table 2).

Calculation of relative differential rates of synthesis. The relative differential rates of synthesis were used to compare the ppm of an individual protein under two growth conditions and are defined as the ratio of the mean for that protein under the two conditions. All relative differential rates of synthesis described in this work are the ratios of the means for the PHN or PLE and PLL samples and the phosphate (PW and PE) samples. A protein with a ratio of 2 is said to be twofold induced, and a protein with a ratio of 0.5 is twofold repressed. Given the variation between gels (as discussed in the previous paragraph) for all proteins with an SE at or below 20% of the mean, a twofold change is significant by the following argument. For a protein with mean counts per minute values for the experimental and control samples of 1,000 ppm and SE at 20% of the mean, the range of means for both would be 800 to 1,200 ppm, and the ratio of the means (1,000/1,000 ppm) would be 1.0. But if the highest value for one and the lowest value for the other were used (1,200/800 ppm), the ratio would be 1.5, or 0.67. For proteins with SEs greater than 20% of the means, a higher threshold value should be used. For proteins for which the SE for both means is 50% of the mean, the ratio could be as high as 4.

Merging data into the *E. coli* gene-protein database. The *E. coli* gene-protein database is a collection of information about *E. coli* proteins largely generated from 2-D gel electrophoresis analysis of whole-cell protein extracts (see reference 50). This is the first study whose results are included in this database to involve measurements of all the proteins detectable on a 2-D gel. Through the matching program within the image analysis software (BioImage, Inc.), all proteins with matches between the reference image (one of the images generated from samples of W3110 grown in ample phosphate) and any other image were assigned a unique match number. An "R" was placed in front of this number to yield a new naming system based on the response-regulation map (RRM name) for all proteins included in this project. This study initiates the response-regulation map of the *E. coli* Gene-Protein Database (see reference 46 for more details). The goal of this project is to identify protein members of various stimulons and regulons. Accordingly, those proteins responding to a particular growth condition are members of the respective stimulon and those proteins responding to a particular genetic control are members of the respective regulon. Previously, all proteins annotated in the database had been given a 2-D protein name called an alpha-numeric (A-N) (34).

Electronic submission of data. Table 3 has been incorporated into the *E. coli* gene-protein database, edition 6.0696, which can be obtained electronically from the database repository at the National Center for Biotechnology Information by anonymous ftp to ncbi.nlm.nih.gov in the directory /repository/ECO2DBASE/ and which will also be available through the World Wide Web (search for ECO2DBASE).

RESULTS

Growth in medium with limited P_i or phosphonate as the only P source. The parameters for examining the pattern of protein synthesis when P_i is limited (P limitation) and during steady-state growth in medium containing either phosphate

TABLE 3. Relative differential rates of synthesis of proteins during phosphate restriction

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f]												MW[g]	pI
								2-fold			3-fold			5-fold			10-fold				
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R0135	C013.5	*uspA*	1,668	1.34	5,079	1.64	1.60													16,039	5.44
R0140	E014.0	*hns*	800	1.73	840	1.25	0.93													14,973	5.56
R0154	C015.4	*mopB*	873	1.53	1,357	2.06	2.05		+	+										16,039	5.47
R0420	E042.0	*tufA*	8,570	1.36	19,230	0.76*	0.94*													44,107	5.70
R0438	F043.8		3,667	1.71	7,376	1.74	1.69													45,386	5.79
R0466	F046.6	*phoA*	188	28.80	290	20.95*	18.74*	+	+	+	+	+	+	+	+	+	+	+	+	46,253	5.78
R0565	B056.5	*mopA*	6,944	1.55	8,809	1.50	1.42													57,243	5.11
R0610	B061.0	*nusA*	641	1.95	944	0.66	0.71													61,193	4.84
R0650	B065.0	*rpsA*	3,645	1.16	4,047	0.78	0.80													68,203	5.11
R0660	B066.0	*dnaK*	4,195	0.84	4,031	1.25	1.26													82,000	5.07
R0840	D084.0	*fusA*	3,327	1.12*	6,254	0.45	0.66		−											84,534	5.56
R1698	D157.0	*rpoB*	1,764	1.65*	2,004*	0.34*	0.44*		−	−										144,055	5.41
R1700	A035.5	*ompC*	7,945*	1.06	12,574	0.72	0.92													33,933	4.80
R1701	A013.0	*rplL*	7,926*	1.06	8,095	0.20	0.20		−	−		−	−		−	−				9,642	4.98
R1703	F014.7	*hns*	1,930	3.94*	3,616	3.43	3.89	+	+	+	+	+	+							14,973	5.83
R1704	H031.3	*pyrB*	5,970*	1.71*	9,918	0.91	0.99													34,400	6.63
R1705			1,079	1.51	1,518	1.54	1.37													21,739	5.97
R1706			272*	2.70*	423	6.32	6.80	+	+	+		+	+		+	+				79,610	6.24
R1707			2,921	0.65	1,266	0.69	0.67													47,455	6.93
R1708	F035.8	*pfkA*	1,659	1.68*	2,847	1.82	1.67													36,281	5.79
R1709			NM	NM	3,848	0.22	0.15		−	−		−	−			−				23,457	4.25
R1710			333	2.60*	462	0.50	0.46	+	−	−										61,811	5.55
R1711			917	0.61*	1,388	0.34	0.24		−	−			−							23,054	7.40
R1714			426	0.90*	554	0.26*	0.38*		−	−		−								113,932	6.20
R1715			796	0.54	1,085	0.37	0.29*		−	−			−							112,277	6.29
R1716			334	0.59*	255	0.61	0.75													98,832	6.28
R1719			543	0.58	844	1.22	1.67													112,277	5.91
R1720			1,778*	0.86*	3,551	0.12	0.22		−	−		−	−		−					113,932	5.71
R1721			267*	1.52	460*	0.93*	1.11*													113,932	5.85
R1722			2,332	1.30	1,812*	0.86*	0.74*													113,932	5.65
R1723			1,462*	1.52	2,625	0.38	0.39		−	−										107,511	5.79
R1725			542	0.74*	693	0.53*	0.22			−			−							100,203	5.65
R1726			691	1.03	1,531	0.24	0.26		−	−		−	−							107,511	5.36
R1727			464	1.26	1,540	0.18*	0.25		−	−		−	−		−					115,621	5.40
R1731	D087.5		1,597	0.92	1,475	0.67*	0.46			−										103,034	5.47
R1733	C137.0	*metH*	214	1.07	317	0.26	0.30		−	−		−	−							127,208	5.20
R1734			129	1.55*	140	0.43	0.47		−	−										68,602	6.45
R1735			95	1.85	101	0.76	0.77													66,701	6.41
R1736			104*	1.09	188	0.34	0.37		−	−										63,314	6.23
R1737	G076.0		320	2.74*	346	4.75	4.82	+	+	+		+	+							58,356	6.19
R1738			372	0.94*	200	1.64	3.62			+			+							94,892	6.24
R1739			426*	1.39*	375	0.65	0.60													91,202	6.08
R1740	G060.1		299*	1.78*	262	2.47	1.80		+											88,874	6.17
R1741			649	1.00*	384	1.77	2.31			+										85,572	5.93
R1742			477	1.00	676	2.09	2.73		+	+										84,520	5.99
R1743			302*	0.87*	308	0.63	0.58													81,506	5.95
R1744			699	1.00*	916	0.70	0.87													80,547	6.06
R1745			193*	0.76*	226*	1.76*	2.05			+										79,610	6.14
R1746	F072.0	*metG*	397	1.23	562	0.49	0.42		−	−										75,000	5.91
R1747	G042.1		192	3.93*	343	5.98	5.87	+	+	+	+	+	+		+	+				70,654	5.98
R1748			268	0.99	341	0.46	0.36		−	−										67,319	6.12
R1749			378	1.45	571	0.58	0.63													67,319	6.19
R1750			659	0.99	938	0.31	0.53		−			−								67,319	6.05
R1751	F050.1	*ilvA*	560	2.70*	934	2.00	2.33	+	+	+										54,999	6.16
R1752			294*	1.31	285	1.75	1.92													54,437	6.10
R1753			765	0.90	684	0.61	0.55													54,999	5.95
R1754			536*	2.21*	372	3.17	3.37	+	+	+		+	+							94,892	5.92
R1755			591	3.57*	535	4.15	8.27	+	+	+	+	+	+			+				97,490	5.81
R1756			553	1.24	602	0.35	0.37		−	−										85,572	5.70
R1757			284*	1.19*	305	2.59	3.28		+	+			+							85,572	5.62
R1758			352*	0.55	261*	0.52*	0.28*			−			−							76,075	5.76
R1759			1,310	0.57	1,567	0.19*	0.25		−	−		−	−		−					76,928	5.70
R1760			325	0.68*	285	0.38*	0.21		−	−			−							76,928	5.62
R1761			307	1.02*	381	0.69	0.66													68,602	5.82

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TABLE 3—*Continued*

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f]												MW[g]	pI
								2-fold			3-fold			5-fold			10-fold				
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R1762			254	1.27	271	0.94	0.57													69,269	5.77
R1763			517	1.43	911	0.28	0.38		−	−		−								64,941	5.72
R1764			365	0.82*	546	0.88	1.11													59,563	5.79
R1765			198	0.81	193	0.55	0.57													59,149	5.72
R1766			163	1.95	272	1.46	1.16													56,227	5.58
R1767	F054.4		1,514	1.14	2,042	0.10	0.03		−	−		−	−		−	−		−	−	56,729	5.87
R1769			295	0.70	158	1.92	1.67													85,572	5.85
R1770	C078.0	*pnp*	1,379	1.09	1,297	0.70	0.59													79,697	5.38
R1771			614	2.01	1,148	0.53*	0.80	+												87,748	5.49
R1773	D078.1		830	1.60	841	0.56	0.53													80,547	5.43
R1774			336*	2.12	732	0.87	1.44	+												72,864	5.32
R1775			133	3.29*	178	1.06	1.22	+			+									69,953	5.39
R1776			83	1.15	100	0.77	0.63													65,512	5.52
R1778			538*	1.68*	717	0.37	0.27		−	−			−							60,875	5.43
R1779			187	1.26*	157	0.74*	0.55*													57,975	5.38
R1780			89*	1.67	199	0.76	0.57													86,648	5.36
R1781			334*	0.76	241	0.34	0.35		−	−										64,941	5.29
R1782	E079.0	*pta*	592	1.99*	1,890*	0.36*	0.32*		−	−			−							79,697	5.48
R1785			1,457	2.40	1,940	0.84	0.89	+												97,490	5.16
R1789			149*	2.39	178	0.96	0.95	+												69,269	5.03
R1790	B058.3	*ptsI*	1,787	2.73	3,631	0.92	1.06	+												61,193	5.03
R1793			69*	3.18	176	0.54*	0.51*	+			+									91,202	4.87
R1794			61	2.89	86	2.85*	2.33	+	+	+										47,945	7.25
R1796			517	1.99*	761	0.44	0.43		−	−										47,693	6.98
R1797			335	1.73*	453	0.76	0.80													52,713	6.58
R1799			165	0.96*	243*	0.64*	0.66													47,455	6.72
R1800			77	4.10*	80*	5.38	5.76	+	+	+	+	+	+		+	+				47,010	6.65
R1801			268	1.31	339	0.34	0.27		−	−			−							53,654	6.38
R1802			568	1.18	721	0.51*	0.64													53,654	6.21
R1803			2,647	1.26	2,471	0.25	0.32		−	−		−	−							51,315	6.34
R1804			1,964	1.21	2,611	0.45	0.47		−	−										50,967	6.27
R1805			96*	1.45*	NM	NM	NM													49,028	6.40
R1806	G051.8		821	0.65	779	0.44	0.45		−	−										49,142	6.33
R1807			734	1.06	648	1.41	1.51													49,142	6.28
R1808			87	1.82	105	1.02	1.02													48,213	6.46
R1809	G052.0	*amn*	269*	1.92*	327	2.46	2.36		+	+										47,693	6.38
R1810			235	1.29	209	1.53	0.71*													47,533	6.21
R1811			1,995	1.47	1,889	0.72	0.52													47,455	6.31
R1812			211*	1.06*	199*	2.56*#	1.16*		+											46,186	6.43
R1813			181	1.67	194	1.90	1.46													48,032	6.31
R1814			391*	0.94*	218	1.90	1.76													51,878	5.88
R1815			561	1.57*	776	1.22	1.00													51,685	6.00
R1816			579	0.50	536	0.34*	0.23	−	−	−			−							49,380	6.08
R1817			3,681	1.03	5,097	0.29	0.25		−	−		−	−							49,260	6.16
R1818	G049.2		2,023	1.44	3,568	0.30	0.23		−	−		−	−							49,028	6.05
R1819			369*	1.54*	595	1.35	1.41													49,028	5.89
R1820			302	1.11	461	0.87	0.76													48,499	5.94
R1821			271	1.54*	355	0.78	1.16													47,613	5.94
R1822			677	1.19*	752	0.83	0.74													47,533	5.90
R1823			442*	0.51	652	0.14	0.13		−	−		−	−		−	−				47,303	6.07
R1824			142	1.13*	128	NR	NR													46,730	6.19
R1825			202*	1.27	450	0.81	0.61													46,524	6.07
R1827			234*	2.71*	218*	2.67	1.05	+	+											46,186	6.08
R1828	F054.1		273	2.22#	515	1.16	1.25	+												56,226	5.84
R1829			393*	0.64	214	1.41	1.33													52,713	5.76
R1830			222	0.91*	218*	1.84	0.95													52,938	5.72
R1831	F050.6		287	2.32*	397	1.77	2.44	+		+										50,800	5.77
R1832			165*	1.56	147	1.09	0.88													50,639	5.83
R1833			583	1.12*	631	1.01	0.74													50,330	5.73
R1836			713	1.16	757	2.75	3.77*		+	+			+							47,693	5.60
R1839			211	1.31*	234	2.02	2.01		+	+										48,213	5.71
R1840			568	2.27*	499	2.24*	2.21	+	+	+										53,169	5.52
R1841			813	2.14	770*	2.68*	2.01*	+	+	+										51,497	5.33
R1843			2,914	1.02	4,779	0.06	0.05*		−	−		−	−		−	−		−	−	50,330	5.43

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TABLE 3—*Continued*

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f]												MW[g]	pI
								2-fold			3-fold			5-fold			10-fold				
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R1844			1,123	0.71	1,114*	0.45*	0.28*		−	−			−							49,505	5.29
R1845	D049.9	*glnA*	6,526	0.74	7,105	0.15	0.09		−	−		−	−		−	−			−	49,028	5.48
R1846			320*	1.58*	401*	16.63*	13.15*		+	+		+	+		+	+		+	+	48,032	5.41
R1847	E049.3		1,378	2.45*	2,029	7.31	7.00	+	+	+		+	+		+	+				47,945	5.53
R1848			916	5.73	1,653	8.14	8.03	+	+	+	+	+	+	+	+	+				47,859	5.47
R1849			315	1.18	442	0.50	0.43		−	−										47,533	5.25
R1850			480	1.44	557	0.81	0.77													47,082	5.36
R1851			200*	1.46	243	0.91	0.42			−										47,010	5.28
R1852			1,567	2.16#	2,940	0.47	0.34	+	−	−										46,524	5.53
R1853			232	0.84*	231	0.61	0.51*													53,408	5.25
R1854			546	2.33*#	1,055	1.14	1.14	+												46,799	5.45
R1855			2,589	1.24	4,077	0.32	0.25		−	−		−	−							46,388	5.46
R1856			855	1.28	1,282*	0.51*	0.64*													51,685	5.41
R1857			464	0.70	379	1.08	1.02													50,639	5.51
R1858			471	1.08	371*	0.56*	0.51*													51,497	5.23
R1859	B050.3	*tig*	4,092	0.97	4,308	0.45	0.26		−	−			−							48,499	5.09
R1860			187	1.51	214	1.97*	2.03*			+										47,155	5.12
R1861	B046.7	*atpD*	4,401	0.76	6,391	0.48	0.31		−	−			−							47,861	5.14
R1862			121*	1.99*	104	1.63	1.62*													43,325	7.32
R1863			303*	1.98	326	3.68	1.99		+			+								41,121	7.37
R1864	H047.4	*gltA*	256*	0.57*	149*	0.59*	0.59*													45,571	6.85
R1865			154*	1.86	203	0.52	0.20			−			−			−				43,690	7.05
R1866			291	2.18	768	0.52	0.36	+		−										40,887	6.99
R1867			99*	1.31	56	1.00*	1.05*													43,866	6.84
R1868	H049.2		881	0.39	1,188	0.62*	0.57	−												46,118	6.52
R1871			126	2.65*	220	1.51*	1.83	+												41,908	6.69
R1872			188*	0.69*	130	0	0		−	−		−	−		−	−		−	−	41,121	6.68
R1873			128	1.79	201	0.60	0.47			−										41,121	6.77
R1875			291	0.81	292	0.70	0.49			−										45,847	6.48
R1876			316	0.86	350	0.83	0.59													45,710	6.42
R1877			2,003	0.33	962	0.38	0.28	−	−	−	−		−							45,288	6.26
R1878			777	2.21	1,184	0.67	0.78	+												44,844	6.40
R1879			5,716	0.94	8,500	0.22	0.29		−	−		−	−							44,995	6.35
R1880			252	1.30	538	0.77	0.59													44,690	6.50
R1881	G043.6	*gdhA*	4,104	0.75	6,782	0.35	0.15		−	−			−			−				44,107	6.31
R1882	G041.4	*carA*	1,221	1.07	2,975	0.40*	0.61		−											42,824	6.24
R1883	H041.0		598	15.19	907	9.08	9.15	+	+	+	+	+	+	+	+	+	+			42,643	6.36
R1885			252	1.17	280	0.98	0.79													41,237	6.26
R1888	G048.0		310	1.24	420	1.48	1.47													46,118	6.18
R1889			520*	1.32	793	0.20	0.17		−	−		−	−		−	−				45,915	6.10
R1890			243*	1.03	168*	1.62*	1.00*													45,143	5.88
R1891	G048.6		1,222	0.40	1,142	0.46	0.28	−	−	−			−							44,995	6.20
R1892			704	1.39*	723	0.80	0.68													44,453	6.09
R1893			211*	2.16*	301*	1.84*	1.22*	+												44,124	5.89
R1894	G044.0	*tyrS*	534*	1.00	1,008	0.73	0.49			−										43,417	5.94
R1896			91*	2.03*	150	0.96	0.71*	+												42,124	5.95
R1897			250	1.18	354	0.83	0.89													41,351	6.01
R1898			381	2.22	626	1.33	1.40	+												41,004	6.10
R1905			3,594	0.81	5,295	0.77*	0.55*													44,207	5.60
R1906	F040.8		246	1.19	373	1.08	0.61													42,195	5.86
R1908			113	1.40*	232	0.85	0.67													41,908	5.79
R1909			399	0.88	489	0.84	0.70*													41,577	5.72
R1910	F039.7	*aspC*	2,006	1.16	2,482	1.22	0.81													41,574	5.86
R1911	F039.6	*aspC*	411	1.79*	713	0.55	0.59													40,648	5.75
R1912	F037.8	*rimL*	340	1.23	568	2.08#	3.05*#		+	+			+							40,400	5.86
R1914	F042.2	*fabB*	11,467*	0.75	10,589	0.70*	0.67*													44,039	5.76
R1915			1,008	1.32*	2,661	0.55*	0.24*			−			−							44,124	5.79
R1916	C043.8	*icdE*	578	0.50	752	0.37	0.23	−	−	−			−							45,915	5.32
R1917			1,648*	0.16*	574	0.30*	0.27*	−	−	−	−	−	−	−						45,847	5.25
R1918			2,356	1.15	4,812	0.54	0.32			−			−							45,288	5.30
R1920	F043.9		4,932	0.87	7,702	0.80	0.94													45,767	5.53
R1922	C042.6	*gnd*	134	2.34	306	4.98	6.11	+	+	+		+	+			+				43,690	5.33
R1923	C041.0		542*	2.65*	1,368	0.51	0.51	+												42,824	5.41
R1925	E039.8	*sucC*	1,227*	1.02	2,881	0.30	0.33*		−	−		−	−							42,439	5.55

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TABLE 3—*Continued*

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f] 2-fold			3-fold			5-fold			10-fold			MW[g]	pI
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R1926			1,808*	2.11	4,777	1.43	1.37	+												42,335	5.35
R1927	F044.2		361	1.29*	451*	1.19*	1.20*													41,577	5.59
R1928	B040.7	*rpoA*	3,106	1.06	5,231	0.47	0.37		–	–										41,799	5.27
R1929	D040.7	*livJ*	3,337	1.05	4,811	0.73	0.50			–										41,577	5.48
R1930			3,203*	0.79	3,436	1.10	1.27*													45,215	5.47
R1931			597*	0.56*	1,108	0.67	0.59*													44,039	5.55
R1932			306	1.36*	454*	2.23*	3.02*		+	+			+							45,915	5.40
R1933	C043.5		327	1.62	358	3.53	3.00*		+	+		+	+							44,124	5.28
R1934			405*	1.07	554	0.85	0.73													44,533	5.27
R1935			465	1.49*	543	0.68*	0.48			–										45,571	5.05
R1937			653	0.77	720	0.57	0.44			–										44,453	5.20
R1938			179	1.35	254	0.74	0.54													43,690	4.96
R1939			158*	2.88*	256	2.73	3.04	+	+	+			+							43,690	5.02
R1940			157	1.01*	124	1.90	1.56													43,417	5.21
R1941			555	2.02*	819	1.15	0.77	+												43,135	5.10
R1942			112	0.00	230	0.64*	0.63*	–			–			–			–			41,689	5.13
R1943			538	0.54	643	0.72	0.97*													41,577	5.19
R1944	A036.1	*dnaN*	1,825	1.96	4,103	0.92	1.32													41,400	4.97
R1945	A048.0		100	1.31	69	2.45	1.30		+											46,118	4.78
R1946			124*	4.97*	176	1.26	1.11	+			+									42,230	4.76
R1947			86*	7.75*	45	8.04	3.90*	+	+	+	+	+	+	+	+					39,784	7.46
R1949			116*	1.34*	146	0.81*	0.48#			–										35,818	7.18
R1950			134*	1.40*	262	0.34*	0.25		–	–			–							39,910	6.94
R1951			105	1.28*	0	0	0													31,914	7.10
R1952			149	1.91	214	1.17*	0.67													40,035	6.55
R1953			128	2.14*	166	1.67	2.45	+		+										39,009	6.67
R1954			434	1.64	529	1.00	0.85													38,610	6.53
R1955			732	3.24*	1,145	3.19	2.88	+	+	+	+	+								38,069	6.63
R1956			814	1.42	1,728	0.53	0.45			–										36,533	6.66
R1957			2,344	0.72*	3,151	0.65	0.73													34,805	6.67
R1958			292	1.28	322	0.99	0.69													32,343	6.58
R1959			259	1.25	375*	0.28*	0.30*		–	–		–	–							32,343	6.64
R1960			284*	0.55*	115	1.10	1.33													33,933	6.77
R1961			997	2.08	1,746	0.54	0.52	+												37,099	6.52
R1962			729	1.76*	1,148	1.17	1.03													39,270	6.20
R1963			378	2.17*	383	1.99	1.85	+												38,341	6.45
R1965	G038.2		288	4.31*	365	5.87	3.33	+	+	+	+	+	+		+					37,128	6.22
R1966			392	1.08	866	0.37*	0.34		–	–										37,657	6.37
R1967			654	1.08	993	0.92	0.67*													35,095	6.48
R1968			317	2.82	418	2.90	2.99	+	+	+										34,224	6.30
R1969			1,297	1.01*	1,732	0.59	0.81													33,353	6.22
R1970			5,114	0.30*	7,122	0.03	0.02	–	–	–	–	–	–		–	–		–	–	32,486	6.50
R1971			560	1.46	628	1.25	1.01													31,914	6.22
R1974	G039.1		150	3.95*	173	4.58	6.31	+	+	+	+	+	+			+				39,009	6.29
R1975			1,069	1.84	1,897	0.41	0.40		–	–										37,379	6.49
R1976			154*	2.40	305	1.15	0.46	+		–										40,160	6.07
R1979			417*	0.87	325	1.05*	0			–			–			–			–	39,270	6.01
R1981	F037.5		136*	2.93*	174*	8.14*	5.43*	+	+	+		+	+		+	+				37,657	5.90
R1982			315	1.76*	563	1.08	0.78													37,518	6.07
R1983			366	0.95	554	0.52	0.37			–										33,353	6.03
R1984			281*	0.98	170	1.03	0.65													33,208	5.88
R1985			1,703	1.25	3,163	0.74	0.45			–										32,774	5.94
R1986	F038.0		3,211	1.32	4,367	1.30	1.39													39,500	5.86
R1987	E029.2		2,708	1.19	3,609	0.69	0.47			–										39,159	5.67
R1988			262	0.89	323	0.58	0.57*													38,341	5.81
R1989			217	2.16	395	1.45	1.13	+												36,817	5.85
R1990	F035.0	*leuO*	332	1.19	461	1.94	2.03			+										34,515	5.77
R1991	F032.5	*ilvE*	1,115	0.52	1,246	0.44	0.33		–	–			–							32,774	5.75
R1993	F037.2		150*	1.40	173*	1.14*	1.02*													36,600	5.70
R1994			1,427*	0.31	1,293	0.96	0.60	–			–									40,160	5.48
R1995			443	1.99*	672	4.32	4.15		+	+		+	+							39,910	5.31
R1996			115*	1.64	137	1.99	1.13													39,657	5.24
R1997			302	1.38	602	0.71	0.67													39,400	5.50
R1998	D040.9		1,137	1.99*	1,651	2.21	2.21		+	+										39,657	5.50

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TABLE 3—*Continued*

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f]												MW[g]	pI
								2-fold			3-fold			5-fold			10-fold				
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R1999	D038.3		504	0.73	572	1.19	0.72													37,414	5.50
R2000			1,085	1.06	1,432	1.25	0.83													38,069	5.46
R2002	E036.6	*pfkB*	206	2.09*	256	3.89	3.04	+	+	+		+	+							37,414	5.59
R2003			450	1.64*	913	0.80	0.77													37,379	5.28
R2004	C037.5		405	1.03	532	0.82	0.90													35,173	5.34
R2005	C036.3		539	1.26	728	1.84	1.62													35,448	5.40
R2006	C035.6		1,052*	1.87*	2,659	0.91	1.13													34,901	5.30
R2007	D035.7		250	1.94	327	8.21	8.95		+	+		+	+		+	+				34,224	5.54
R2008	D033.4	*htpH*	176*	1.79*	317	6.17	4.79		+	+		+	+		+					34,100	5.59
R2009			622*	1.06	596	0.97	1.07													32,200	5.36
R2010	D031.5	*trxB*	364	1.04	647	0.63	0.50*			−										31,630	5.53
R2011	D032.5		1,821	1.16	1,709	0.39	0.36		−	−										33,301	5.47
R2012			122*	1.48	159	1.28	0.62													39,784	5.10
R2014			970	0.91	1,948	0.58	0.49			−										35,240	5.08
R2015	B036.0	*ompF*	4,981*	0.52	9,771	0.11	0.08		−	−		−	−		−	−			−	34,700	4.93
R2016			344	3.25	593	0.92	1.24	+			+									33,643	5.09
R2017			145*	3.53*	200	1.02	1.30*	+			+									32,774	4.97
R2018			68	1.92*	114	1.24	1.02													38,610	5.14
R2019			55	6.24	163	1.64	0.72	+			+			+						36,248	4.75
R2020			387*	0.88	560	0.74	0.70													33,353	4.70
R2021			274	1.76	538	0.77	0.70													38,206	4.87
R2023			695	1.07	647	0.96	0.49			−										27,797	7.27
R2025			1,005	0.62*	1,632	0.48	0.49		−	−										24,220	7.34
R2026			172	1.46*	240	0.95	0.56													25,811	7.24
R2027			144*	1.35*	186	1.03	0.77													28,162	6.88
R2031			196	1.72	213	0.80	0.79*													30,929	6.54
R2032			63	3.96*	192	3.03	3.36	+	+	+	+	+	+							30,514	6.76
R2033			98*	2.67	210	4.37	5.44	+	+	+		+	+			+				29,175	6.55
R2034			1,365	0.84	2,177	0.32	0.30		−	−		−	−							28,535	6.63
R2036			1,400	2.24*	1,901	1.75	2.24	+		+										28,162	6.76
R2038			306	1.16*	380	0.72	0.74													26,648	6.57
R2039			176	1.24	252	0.73	1.22													26,432	6.65
R2040			180	1.87*	234	3.65	2.91		+	+		+								26,220	6.78
R2041			121	1.90*	717*	0.37*	0.25*		−	−			−							25,712	6.57
R2042			614*	1.58*	881	1.37	1.05													31,348	6.42
R2043			206*	1.26*	284	0.98	0.51													29,569	6.22
R2044			345	1.50*	342	1.27	1.42													29,437	6.32
R2045			919	1.26	1,393	0.68	0.71													29,045	6.46
R2046			355	1.96	637	1.35	1.43													28,410	6.28
R2047			361	1.00*	818	0.26*	0.18		−	−		−	−			−				28,162	6.38
R2048			185*	20.01	293	7.66*	11.39	+	+	+	+	+	+	+	+	+	+		+	27,917	6.48
R2049			248	1.38	331	1.06	1.19													27,917	6.21
R2050			382	1.44	656	0.24	0.19		−	−		−	−			−				26,869	6.34
R2051			250	1.29	419	0.47	0.54*		−											26,648	6.45
R2052			204	2.35*	424	0.95	1.25*	+												25,614	6.43
R2053			270	1.58	324	4.41	3.97		+	+		+	+							25,143	6.36
R2054			527	1.35	779	1.73	1.86													24,789	6.42
R2056			824	1.62*	1,217	3.43	3.78		+	+		+	+							24,297	6.29
R2057			212	1.25	208*	1.67*	1.46*													30,929	6.15
R2058			259	2.22	921*	1.64	0.93	+												30,929	5.95
R2059			6,544	1.30	7,433	1.08	1.20													30,929	5.88
R2060			447	0.93	696	0.71	0.81*													30,514	6.06
R2061			409	10.20*	670	10.90	12.63	+	+	+	+	+	+	+	+	+	+	+	+	29,569	5.91
R2062			1,480	1.90	3,425	1.17	1.10													29,569	5.99
R2063			413	1.19	485	1.58	1.12													29,175	6.07
R2064	G032.0		1,638	1.54*	2,125	1.65	1.83													28,800	6.10
R2065	G030.1		364	1.20	515	1.40	1.82													26,013	5.99
R2066	G029.5		552	2.11*	760	1.74	1.45	+												25,422	6.05
R2067			131	1.98*	152	1.85	1.97*													24,297	6.07
R2068			151*	1.02	340	0.53	0.44			−										25,422	6.19
R2069			1,990	0.83	1,653	1.52	1.37													30,929	5.65
R2070	F033.1	*ompA*	235	1.19	257	0.77	0.68													29,437	5.68
R2071			1,185	0.60	1,187	0.34	0.21		−	−		−								28,039	5.71
R2072			437	0.93	693	0.69	0.35			−										27,559	5.76

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TABLE 3—*Continued*

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f] 2-fold			Induction of protein[f] 3-fold			Induction of protein[f] 5-fold			Induction of protein[f] 10-fold			MW[g]	pI
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R2073	F030.3		184	1.39*	311	2.47#	2.19#		+	+										26,869	5.84
R2074			170*	1.55*	250	1.31	0.88													26,539	5.65
R2075			125	3.88	175*	4.38*	3.27*	+	+	+	+	+	+							26,220	5.72
R2076			207	3.45*	218	4.23	4.33	+	+	+	+	+	+							25,811	5.59
R2077			368	1.33	617	0.79	0.59													24,456	5.69
R2078			387	9.10*	664	10.63	10.92	+	+	+	+	+	+	+	+	+		+	+	25,811	5.85
R2079			1,365*	0.16	6,343*	0.04*	0.05*	−	−	−	−	−	−	−	−	−		−	−	28,535	5.84
R2080	F028.0	*ompA*	1,522	1.01	3,125	0.38	0.31*		−	−			−							24,297	5.90
R2081	F026.0	*adk*	370	1.45	490	2.53	2.48		+	+										24,963	5.87
R2082			259	1.63	330	3.85	3.49		+	+		+	+							29,437	5.86
R2083			1,036*	0.80	1,050	0.67	0.95													31,068	5.35
R2084			437	1.02	612	0.83	0.56													29,836	5.32
R2086			363	1.16	538	1.45	1.49													28,285	5.39
R2087			344	1.27	556	1.17	1.19													26,539	5.51
R2088			645	1.05	926	0.39	0.43		−	−										26,116	5.26
R2089	D029.8		1,116	2.94*	1,524	3.71	3.16	+	+	+		+	+							25,712	5.49
R2090	C029.1		298	1.39	407	1.90*	1.69													24,963	5.40
R2091	D028.3		1,024	1.02	1,255	1.40	1.48													24,963	5.49
R2092	D028.0		316	16.19	375	2.95	2.55	+	+	+	+			+			+			24,297	5.52
R2096			167*	1.04	225	0.93	1.16*													29,437	5.40
R2097			1,813*	0.67*	714	0.75	0.74													31,068	5.47
R2098			263*	0.86*	229	0.94	0.64													27,797	5.46
R2099			274*	0.93	356	0.82	0.87*													31,068	5.16
R2100	B033.0		1,233	1.65	2,219	1.05	1.30													30,929	5.23
R2101	B035.1		301	2.04*	805	0.63	0.53	+												30,000	5.05
R2102	A033.7		147	1.48	203	0.64	0.52*													29,045	4.95
R2103			193	2.62*	281	0.95	0.74*	+												28,410	5.12
R2104			158	2.90	224	1.43	1.46*	+												26,981	5.11
R2105			150	1.04*	111	3.56	3.87		+	+		+	+							26,013	5.09
R2106			361	0.85	537	0.58	0.66													25,912	5.03
R2107			175	3.42	282	5.66	5.05	+	+	+	+	+	+		+	+				25,422	5.14
R2108			388*	1.70	309	1.86	1.46													24,704	5.13
R2109			166	2.75	305	1.47	1.39	+												29,836	4.86
R2110			76	3.80	174	2.05	2.15	+	+	+	+									28,410	4.90
R2111	A028.0	*cheZ*	118	2.47*	206	0.76	0.81	+												25,422	4.90
R2112			54	3.28*	103	1.23	1.01	+			+									29,306	4.67
R2113			106	2.71*	120	1.50	1.42*	+												23,457	7.34
R2114			181*	4.61*	272	2.31	1.85*	+	+		+									23,002	7.31
R2115			292	1.98*	578	0.57	0.26			−			−							22,670	7.31
R2116			204	1.90	241	0.81	0.86													21,978	7.35
R2117			558*	1.09*	789	0.80	0.55													21,997	7.22
R2118			175	1.56*	218	1.09	0.61*													23,335	6.95
R2120			97	2.57	182	0.66	0.78*	+												22,547	6.95
R2121			580	0.74	862	0.67	1.41*													22,038	7.02
R2122			695	4.03*	1,474	0.38	0.22	+	−	−	+		−							23,520	6.64
R2124			144	1.56	209	1.25	1.33													23,227	6.55
R2125			127*	1.17*	165	1.15*	0.97*													22,759	6.80
R2126			539	1.01	856	0.58	0.38*#			−										22,628	6.53
R2127			201*	1.13*	185	1.09	0.92													22,331	6.65
R2128			3,405	0.64*	3,606	0.91	0.97*													21,978	6.82
R2129			491	1.73	485	0.73	0.71													21,960	6.60
R2130			137*	5.15*	135	9.88	8.40	+	+	+	+	+	+	+	+	+				21,798	6.67
R2131			165	4.11*	201	2.95	2.23*	+	+	+	+									24,069	6.40
R2132	G027.1		1,681	1.56	2,190	1.22	0.81													25,745	6.20
R2133			97	1.99	200	0.64	0.73*													23,335	6.41
R2134	H027.4		316	1.21	452	0.51	0.45			−										23,219	6.50
R2135			1,133	1.12	1,544	0.65	0.65													22,714	6.25
R2136			299	1.65	435	1.21	1.14													22,508	6.30
R2137	G024.7		322	1.55	413	2.80	3.40		+	+			+							22,100	6.16
R2138			241	1.61	230	1.89	2.11			+										21,978	6.35
R2139			440	1.47	701	1.49	1.57													21,857	6.39
R2141	G023.4		138	2.44	252	5.02	6.68	+	+	+		+	+		+	+				21,830	6.25
R2142			187*	1.26*	195	1.33	1.27*													23,002	6.31
R2143	G027.0		936	1.40	1,241	1.76	1.79													23,520	6.06

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TABLE 3—*Continued*

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f]: 2-fold			3-fold			5-fold			10-fold			MW[g]	pI
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R2144	G025.8		302	1.50*	393	1.95	1.89													22,805	6.11
R2145			201*	1.86	232	1.12	0.90													22,805	6.03
R2146	F027.0		313	1.11*	502	0.62	0.85													22,508	5.90
R2147	F022.5	*eda*	1,630	2.89*	2,676	3.16	3.14	+	+	+		+	+							22,156	5.88
R2148			142	1.38*	490*	0.58*	0.68													22,130	6.02
R2149			6,838	1.49*	10,771	1.29	1.21													23,649	5.90
R2150	G028.0	*glpR*	385	1.55	575	1.00	NR*													23,853	6.16
R2154	F025.8		881	1.71*	1,271	1.99	1.67													24,414	5.75
R2155			296	1.10	365	0.63	0.44*			−										22,156	5.62
R2157	F024.6		735	1.10	1,064	0.82	0.74													23,108	5.85
R2160	C027.1		930*	0.58	687	0.56	0.51*													25,569	5.41
R2162			2,544	1.56	5,356	0.07*	0.09*		−	−		−	−		−	−		−	−	23,520	5.32
R2163	D027.1	*sspA*	810	1.20	1,150	0.87	0.85													23,277	5.53
R2164			500	1.18	767	1.28	1.62													23,108	5.41
R2165	C026.8	*atoA*	194	30.38	437	14.93	17.75	+	+	+	+	+	+	+	+	+	+	+	+	22,852	5.41
R2166	C025.2		463	1.71*	537	3.08	1.69		+			+								22,587	5.43
R2167			500	2.23*	762	2.60	2.35	+	+	+										22,547	5.30
R2169			353	0.99	413	0.67	0.53*													22,130	5.24
R2170	E022.8		3,337	1.05	4,833	0.34	0.26*		−	−			−							22,100	5.55
R2171			664	1.74	1,259	0.96	0.85													22,038	5.34
R2172			334	1.50	606	0.97	1.33													21,870	5.31
R2173			258	1.38	302	1.48	1.28													21,846	5.55
R2174			198	2.89*	385	1.50	1.64	+												23,002	5.50
R2176	B025.3	*grpE*	1,037	1.11*	1,710	1.48	1.67													22,759	5.08
R2177	B024.2		299	1.21	388	0.95	0.97													22,182	5.13
R2178	A041.3		190*	1.10*	247	0.35	0.35*		−	−										22,182	4.98
R2180			178	2.25	329	1.28	1.26	+												21,870	5.23
R2181			261	1.39	481	0.89	0.66													23,002	4.92
R2182			536	1.57	812	1.38	1.53													22,331	4.92
R2183			186	2.21	292	1.29	1.06	+												22,130	4.64
R2184			92*	1.21*	180*	0	0		−	−		−	−		−	−		−	−	21,566	7.27
R2185			1,158	1.11	1,602	0.87	0.73													21,728	6.85
R2186			1,017	0.96	1,351	0.93	0.78*													21,645	6.67
R2187			179	2.42*	253	2.90	3.35	+	+	+			+							21,466	6.55
R2188			476*	1.21*	606	0.61	0.58													21,686	6.66
R2189			80*	2.68	162	1.89	1.44	+												21,728	6.35
R2190			83	2.67	134	2.12	1.91	+	+											21,752	6.04
R2191	F020.9		104*	2.61	168	2.52	2.65	+	+	+										21,724	5.98
R2192	F017.7		318	1.86	468	1.98	1.94													21,446	5.90
R2193	F018.8	*ssb*	769	0.87	1,409	0.20	0.12*		−	−		−	−		−	−				21,425	6.02
R2194			81*	2.04	118	1.96	1.58	+												21,765	5.79
R2195	E021.1	*dsbA*	583	1.57	987	1.22	1.17													21,780	5.68
R2196			101	2.31	182	0.91	0.80	+												21,745	5.58
R2197			111*	2.60	169	1.98	2.00	+		+										21,726	5.57
R2198			256	1.59	332	0.85	0.65													21,726	5.79
R2199			166	1.82	326	0.71	0.57													21,722	5.73
R2200	E018.0		998	1.22*	1,103	2.96	2.44		+	+										21,425	5.61
R2201			160	3.02*	283	2.85	2.97	+	+	+	+									21,771	5.28
R2202	C023.0		506	1.47	586	1.05	0.64													21,780	5.47
R2203	C022.7		623	1.01	1,023	0.72	0.70													21,780	5.36
R2204	B020.9	*ahpC*	4,435	2.24	7,750	1.75	1.92	+												21,728	5.30
R2205			130	1.40	192	1.31	1.01													21,626	5.50
R2206	C018.0		1,804	2.32*	2,719	3.48	3.35	+	+	+		+	+							21,490	5.44
R2207			503	1.10*	525	1.93	1.79													21,466	5.31
R2208			327	0.89	607	0.59	0.96*													21,760	4.95
R2209			215	1.45	212	1.55	1.57													21,765	5.03
R2210			365	1.74*	536	1.91	1.75													21,739	5.13
R2211			761	1.51	1,725	0.81	0.97													21,733	5.22
R2212			722	0.92	790	0.80	0.78													21,636	4.95
R2213			1,493	1.49	1,873	1.54	1.62													21,403	5.07
R2214			158*	1.52*	204	1.03	0.62													21,380	5.15
R2217			150	2.69	271	1.77	1.26	+												20,664	7.17
R2218			1,459	0.81*	2,047	0.03*	0		−	−		−	−		−	−		−	−	20,284	7.28
R2221			959	1.53	1,376	1.74	1.62													20,223	6.53

Continued on following page

TABLE 3—*Continued*

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f] 2-fold			3-fold			5-fold			10-fold			MW[g]	pI
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R2222			228	2.09	436	0.96	0.93	+												17,699	6.55
R2225			617	0.92	912	0.25	0.08*		–	–		–	–			–			–	21,356	6.22
R2226			212	2.09	217	4.00	3.26*	+	+	+		+	+							20,713	6.20
R2227	G016.4		432	1.33	627	1.48	1.55													20,713	6.36
R2228			89*	4.41*	227	5.59	4.92	+	+	+	+	+	+		+					20,563	6.27
R2229	G015.8	*fur*	1,619	5.27*	2,082	7.96	9.69	+	+	+	+	+	+	+	+	+				17,792	6.19
R2230			0	305	142	3.18	3.59	+	+	+	+	+	+	+			+			18,113	6.47
R2231			65*	5.16*	85	18.00	20.56	+	+	+	+	+	+	+	+	+		+	+	21,155	5.92
R2232			1,442	1.36	2,231	1.23	1.26													20,510	5.87
R2234			86	2.37*	135	1.09	0.61	+												20,563	5.75
R2235			934	1.12*	566	2.75	2.50		+	+										20,893	5.53
R2236			1,491	1.88	2,614	2.25	2.90		+	+										20,850	5.37
R2237			222*	0.95	252	0.87	0.93													20,510	5.51
R2238			473	1.76	612*	1.06	1.12													19,685	5.34
R2239			648	1.35	750	1.96*	1.73*													18,691	5.53
R2240			272	1.28	382	2.73	3.43		+	+			+							17,804	5.29
R2241	C015.3	*rpsF*	713*	0.99	1,339	0.26	0.20*		–	–		–	–			–				17,400	5.47
R2243			294	1.12	284	0.98	0.58*													19,829	5.01
R2244	A017.6	*greA*	105*	1.22	136	1.37	1.43													19,829	4.95
R2245	B015.0		1,036	1.91	1,872	1.28	1.21*													18,113	5.08
R2246	B014.5		492*	10.60*	1,390	6.59	6.13*	+	+	+	+	+	+	+	+	+	+			17,804	5.11
R2247			200	1.46	205	0.87	0.84													19,800	4.88
R2248			59*	4.35*	68	2.89	4.27	+	+	+	+		+							17,908	4.92
R2249			725	1.40	1,096	0.24	0.17*		–	–		–	–			–				15,723	6.65
R2251			209*	2.49	245*	5.17*	5.18*	+	+	+		+	+		+	+				10,027	6.59
R2252			935	6.62*	1,467	0.22	0.26	+	–	–	+	–	–	+						13,158	6.79
R2253	H014.0	*rplI*	297	2.28#	401*	0.86*	0.51*	+												14,832	6.19
R2254			222*	1.76	314	0.98	0.94*													13,030	6.20
R2255			273*	0.85	266	1.32	1.18*													12,161	6.25
R2256	G012.4		666	1.48	689	1.55	1.62													10,092	6.37
R2257	G014.1		336	2.38*	260	8.22	10.75	+	+	+		+	+		+	+			+	14,449	6.13
R2258			480	1.08	509	0.57	0.18*			–			–			–				13,030	5.99
R2261	F013.0		1,031	1.25	979	2.42	2.82		+	+										12,000	5.82
R2262	F012.3		772	0.97	1,024	0.27	0.25		–	–		–	–							10,745	5.86
R2263	C014.3	*bfr*	746	1.42	903	1.30	1.39													16,350	5.34
R2265	C014.7	*ibpB*	314*	1.05*	308	0.37	0.66*		–											14,832	5.47
R2267			846*	0.85	631	2.03	2.13		+	+										16,093	5.14
R2269			304	2.41	293	3.68	4.59*	+	+	+		+	+							9,679	7.07
R2270			189	1.86	334	0.90	0			–			–			–			–	9,808	6.31
R2271			91*	0.62*	134*	0*	0*		–	–		–	–		–	–		–	–	7,600	6.35
R2272			56	3.40	79*	1.70*	1.14*	+			+									8,300	6.40
R2273			95*	3.51*	50	5.55	2.77*	+	+	+	+	+			+					9,693	6.20
R2274			200*	2.29*	383	2.27	1.65*	+	+											9,617	6.06
R2275	F007.0	*ptsH*	1,348	2.23	2,678	0.79	0.83	+												9,390	6.11
R2280			1,317	1.61	2,290	5.44	9.44		+	+		+	+		+	+				8,900	5.02
R2282			350*	2.20*	229	3.54	3.85	+	+	+		+	+							9,609	4.82
R2283			144	1.77	262*	0.91*	1.40													70,654	5.16
R2284			320	1.22	424	0.39	0.41		–	–										69,953	5.10
R2285	C062.5	*htpG*	1,002	0.91	1,197	0.64	0.45			–										64,000	5.36
R2289			365	1.66	843*	0.70	0.54													66,701	5.21
R2290	C062.7	*aceF*	419	1.45	843	0.65	0.55													69,016	5.26
R2291	C070.0	*aceF*	419	1.45	843	0.65	0.55*													72,508	5.26
R2292	B013.0	*rplL*	866	0.57	1,080	0	0		–	–		–	–		–	–		–	–	9,700	5.06
R2296	C013.4	*uspA*	70*	3.12	153	1.39*	0.52*	+			+									11,500	5.35
R2302			459*	2.08*	471	2.27	2.18	+	+	+										9,390	5.12
R2303			2,073	0.92	1,565	0.29	0.22		–	–		–	–							6,800	4.98
R2304			0	0	0	100	100		+	+		+	+		+	+		+	+	12,652	4.88
R2305			0	322*	0	1,493	1,900	+	+	+	+	+	+	+	+	+	+	+	+	14,707	5.28
R2307	C014.8	*rpsF*	2,643	0.87	4,904	0.08	0.18		–	–		–	–		–	–		–		17,000	5.56
R2308	D014.7	*rpsF*	2,010	0.74	3,188	0	0		–	–		–	–		–	–		–	–	16,390	5.63
R2309			0	1,079*	0	0	0	+			+			+			+			17,908	5.50
R2313			0	499.5*	135*	1.37	1.28	+			+			+			+			11,143	5.51
R2317			337*	1.22*	0	496	594		+	+		+	+		+	+		+	+	18,691	5.34
R2318			53*	2.59*	79	2.74	3.01	+	+	+			+							20,098	5.23

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TABLE 3—*Continued*

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f]												MW[g]	pI
								2-fold			3-fold			5-fold			10-fold				
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R2319			50*	3.72*	112	4.75	4.69	+	+	+	+	+	+							18,599	5.00
R2320			0	0*	0	162	137		+	+		+	+		+	+		+	+	16,093	5.01
R2321			0	143*	0	221	181	+	+	+	+	+	+	+	+	+	+	+	+	15,219	4.90
R2327			1,127	1.55	1,696	1.42	0.84													9,200	5.27
R2328			0	0*	0	967	900*		+	+		+	+		+	+		+	+	9,808	5.19
R2330			139	5.68	320*	4.20*	4.80	+	+	+	+	+	+	+						10,841	5.17
R2336			2,992	0.81	3,919	0.68	0.30			−			−							20,806	5.64
R2337	G016.0		66*	8.44*	97	14.58	16.48	+	+	+	+	+	+	+	+	+		+	+	19,535	5.96
R2338	G015.1		0	431*	63	2.71*	2.49*	+	+	+	+			+			+			18,011	6.00
R2339			19*	15.74*	0	323	292	+	+	+	+	+	+	+	+	+	+	+	+	19,611	6.02
R2340			360*	0.74*	NR	391	417*													21,604	5.89
R2343			480*	0.89	416	0.000	0.36*		−	−										20,806	5.59
R2345	B020.0	*folA*	63*	4.42*	158	2.42	2.13	+	+	+	+									21,670	5.29
R2346			88*	4.21*	189	1.51	1.54	+			+									21,717	5.23
R2349			0	87*	0	224	197	+	+	+	+	+	+	+	+	+	+	+	+	21,711	5.70
R2351			497	1.03	629	0	0		−	−		−	−		−	−		−	−	21,580	5.02
R2352			94*	3.49*	165	0.37	0	+	−	−	+		−			−			−	21,695	4.97
R2354			594	5.16*	944	0.35	0	+	−	−	+		−	+		−			−	22,714	5.48
R2356			415	1.00*	415	9.41	9.01		+	+		+	+		+	+				22,587	5.59
R2357	D025.5		1,048	2.20	1,253	2.54	4.34	+	+	+			+							22,508	5.48
R2358			380*	1.00*	350	1.44	1.52													23,163	5.35
R2360			167	1.40	209	1.84	1.35													9,500	5.53
R2361			590	0.58	615	0.32	0.18		−	−		−	−			−				9,614	5.60
R2362			429*	0.76	258	1.63	0.51*													9,400	5.66
R2364			74*	2.06*	121*	2.48*	0.93*	+	+											8,000	5.85
R2365	F010.1	*htpK*	66*	3.52*	267*	3.38*	1.47*	+	+		+	+								7,500	5.98
R2366	G010.7		437	2.57	594	2.75	3.00	+	+	+			+							8,600	6.18
R2369			307*	2.65	304	10.60	11.25	+	+	+		+	+		+	+		+	+	7,500	5.39
R2371			205*	3.04*	337	1.05	0.90	+			+									8,000	5.53
R2374			0	295	0	354	252*	+	+	+	+	+	+	+	+	+	+	+	+	13,931	5.20
R2375			319	1.23	366	1.08	1.07													9,642	5.26
R2384			373	1.99*	870	0.92	1.00													45,779	5.74
R2385			0	5,848*	706*	3.14*	2.76*	+	+	+	+	+		+			+			46,051	5.75
R2386			207*	12.26*	444	6.29*	3.21	+	+	+	+	+	+	+	+		+			46,456	5.80
R2387			0	0	0	1,159	877		+	+		+	+		+	+		+	+	46,661	5.77
R2388	F049.0		230	7.62	263*	8.04*	5.99*	+	+	+	+	+	+	+	+	+				46,456	5.74
R2389			266	5.26*	484	1.79	2.39	+		+	+			+						46,456	5.63
R2390			0	755	0	901	640	+	+	+	+	+	+	+	+	+	+	+	+	46,524	5.61
R2394			1,490	1.94*	3,710	0.55	0.43*			−										45,359	5.43
R2395			1,168	1.17	2,336	0.47	0.32		−	−			−							44,533	5.32
R2396			8,389	1.07	11,507*	0.82*	0.67*													45,215	5.36
R2399			475*	1.63*	659*	0.48*	0		−	−			−			−			−	46,730	5.43
R2400			2,231	0.36	937	0.49*	0.39*	−	−	−										46,456	5.41
R2401			545	1.13*	663	0	0		−	−		−	−		−	−		−	−	46,592	5.23
R2402			113	1.58	133	1.43	0.90													47,693	5.17
R2404			33*	5.11	0	136*	151*	+	+	+	+	+	+	+	+	+		+	+	46,253	5.04
R2405			0	170	0	0	0	+			+			+			+			44,920	5.07
R2406			118*	1.61	151*	1.73*	1.51*													48,306	4.99
R2410			204	0.41	300	0	0	−	−	−		−	−		−	−		−	−	44,290	5.00
R2411			129	1.82*	240*	0.80*	0.56*													49,505	5.20
R2412			124	3.99*	NR	845*	748*	+			+									47,945	5.35
R2414			4,478*	0.12*	1,621	0.17*	0.05*	−	−	−	−	−	−	−	−	−			−	49,260	5.43
R2415			162*	3.10	401	0.36	0.24*	+	−	−	+		−							54,168	5.11
R2416			65*	7.16*	63	7.64	6.93	+	+	+	+	+	+	+	+	+				50,330	4.86
R2419			239	3.76*	0	942	763*	+	+	+	+	+	+		+	+		+	+	107,511	5.50
R2420			1,133*	0.82	1,487	0.38	1.60*		−											103,034	5.52
R2421	F084.1	*clpB*	520	2.49	768	2.51	3.76	+	+	+			+							107,511	5.59
R2422			191*	1.14*	113	1.05	1.15													79,610	5.49
R2423			119*	1.04*	0	100	144		+	+		+	+		+	+		+	+	84,520	5.55
R2424	D088.0		430*	1.68	431	0.91	0.79													105,987	5.42
R2425			1,326*	0.64	NR	878.00*	NR													113,932	5.43
R2428			0	458	0	116	245	+	+	+	+	+	+	+	+	+	+	+	+	91,202	5.38
R2431	E140.0		2,053	0.65	3,478	0.06*	0.10*		−	−		−	−		−	−		−	−	132,499	5.47
R2432			2,540	1.57	7,428	0.29	0.16		−	−		−	−			−				112,277	5.45

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TABLE 3—*Continued*

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f]: 2-fold			3-fold			5-fold			10-fold			MW[g]	pI
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R2433			204*	0.99	375	0	0		–	–		–	–		–	–		–	–	45,641	6.17
R2437			1,653*	3.23*	2,119	3.48	2.23	+	+	+	+	+								43,779	6.16
R2442			504	0.57	226*	0.95*	0.51*													44,039	5.97
R2444			222	109*	334	0	0		–	–		–	–		–	–		–	–	38,069	5.86
R2445			0	0	0	379	396		+	+		+	+		+	+		+	+	40,283	5.79
R2446	F039.0	*argI*	996	1.01	1,379	0	0		–	–		–	–		–	–		–	–	38,864	5.76
R2447			155*	1.18	208*	0.64*	0.51*													41,577	5.62
R2449			457	1.99*	1,113*	1.20*	0.48*			–										40,768	5.58
R2450	E038.5		2,819	1.46	1,687*	1.42*	0.88*													39,753	5.58
R2454			256	2.13	342	0.86*	0.76*	+												43,509	5.56
R2455			0	0	207*	0	0		–	–		–	–		–	–		–	–	43,509	5.51
R2456			689*	0.70	1,012	0.57	0.51*													41,577	5.38
R2457	C039.3	*recA*	645*	1.92*	1,317	1.21	1.02													41,121	5.38
R2458			353	0.51*	352	0	0		–	–		–	–		–	–		–	–	40,648	5.43
R2459			0	4,825	0	508	356*	+	+	+	+	+	+	+	+	+	+	+	+	36,105	5.29
R2460			79*	9.85*	111*	1.80*	1.46*	+			+			+						36,248	5.22
R2461			664	1.34	1,206	0.12	0		–	–		–	–		–	–			–	37,239	5.08
R2462			371	1.52	944	0.86	0.82													36,533	5.11
R2463	B037.0	*phoE*	165*	48.45	127	38.67	32.85	+	+	+	+	+	+	+	+	+	+	+	+	33,933	5.06
R2464			133*	24.86	0	826	632	+	+	+	+	+	+	+	+	+	+	+	+	34,515	5.01
R2465			547*	1.22*	671	0.82	0.59													35,240	4.76
R2466			0	0	0	461	458		+	+		+	+		+	+		+	+	27,095	5.24
R2467			206*	1.26*	201*	2.56*	2.08*		+	+										25,912	5.41
R2468			1,525*	0.64	1,228	0.32	1.40*		–			–								23,996	5.48
R2469			511*	1.97	660*	1.26*	1.16*													23,520	5.47
R2470			281	1.32*	382	0.79	0.51*													23,335	5.56
R2471			674	0.62	1,003	0.51*	0.51*													25,422	5.36
R2472			0	249	0	565	570	+	+	+	+	+	+	+	+	+	+	+	+	24,456	5.32
R2473			735	1.25	1,258	0.74	0.66*													22,587	5.23
R2474			389	1.52	685	0.56	0.77*													23,520	5.22
R2475			341*	0.88	598	0.00	0.48*		–	–		–			–			–		23,520	5.26
R2476			812*	0.95	1,047	0.38	0.24		–	–			–							23,853	5.14
R2477	B028.3		367*	0.65*	0	408	440		+	+		+	+		+	+		+	+	23,277	5.11
R2478	E032.1		469	1.12	969	0.21	0.22*		–	–		–	–							30,080	5.58
R2479			353*	1.16*	240	3.08	2.86		+	+		+								28,410	5.57
R2480	C031.6	*tsf*	5,345	0.92	7,444	0.39	0.37		–	–										31,770	5.43
R2481	C030.7	*tsf*	408*	NR	1,149*	0.50*	0.44*		–	–										31,276	5.50
R2482			238*	1.64*	344	NR	NR													31,630	5.30
R2484			241	0.89*	403	0.00	0.00		–	–		–	–		–	–		–	–	36,400	5.59
R2490			376	0.00	323*	1.25*	0.65*	–			–			–			–			28,285	5.64
R2491			588	1.27	541	0.58														27,797	5.66
R2492			826	1.22	1,362	1.22*	1.47*													29,702	5.78
R2494			275*	1.81*	0															30,652	5.81
R2498			1,344*	1.26	1,041	1.27	0.90													27,917	5.89
R2499			0	194*	0	311	412*	+	+	+	+	+	+	+	+	+	+	+	+	27,441	5.94
R2501			0	0	151	4.40	3.85		+	+		+	+							23,163	5.94
R2503	G036.2		0	297*	0	304	239*	+	+	+	+	+	+	+	+	+	+	+	+	25,614	5.98
R2504			0	500*	0	369	348*	+	+	+	+	+	+	+	+	+	+	+	+	26,432	5.89
R2507			508	0.92	730	0	0		–	–		–	–		–	–		–	–	22,670	6.34
R2508			349	0.68*	310	0	0		–	–		–	–		–	–		–	–	23,520	6.31
R2509			0	0	168	0	0		–	–		–	–		–	–		–	–	21,978	6.08
R2510			66	2.29	89	3.62	3.98	+	+	+		+	+							21,815	6.06
R2513	G029.2		158*	1.45	199	0.85	0.51*													27,458	6.01
R2514			289*	1.43*	540	0	0		–	–		–	–		–	–		–	–	23,335	5.77
R2516			227*	0.71*	435*	0	0		–	–		–	–		–	–		–	–	22,038	5.78
R2517			294	1.41	545	0	0		–	–		–	–		–	–		–	–	26,539	6.39
R2520			351	1.25	495	1.20	1.36													30,652	6.43
R2522			314*	1.56	221	1.27	1.79*													28,410	6.17
R2523			0	471	0	848	917	+	+	+	+	+	+	+	+	+	+	+	+	32,486	6.24
R2524			704	1.34	632	0.63	0.39*			–										36,817	6.19
R2525			0	0	446*	0.67*	0.63*													36,248	6.21
R2526			118*	0.96	118	0.76*	0.00			–			–			–			–	35,240	6.08
R2527			204*	0.90	175	0	0.61*		–			–			–			–		32,343	6.16
R2528			1,024	0.44*	1,447*	0	0	–	–	–		–	–		–	–		–	–	38,069	6.00

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TABLE 3—*Continued*

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f] 2-fold			3-fold			5-fold			10-fold			MW[g]	pI
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R2529			479	3.34*	915	3.35	2.72*	+	+	+	+	+								40,283	5.91
R2530			295*	0.49	293	0	0	−	−	−		−	−		−	−		−	−	40,768	5.96
R2532			553	0.64	450	1.99*	0.67*													43,039	5.98
R2534			478	1.03	573	0	0		−	−		−	−		−	−		−	−	43,135	5.80
R2538			1,669	1.18	1,836	0.26	0.54		−			−								38,877	6.12
R2539			565	1.04*	785	1.96	1.24													41,237	6.18
R2540			195*	1.86*	238*	0.97*	0.51*													41,799	6.11
R2543			421*	0.90	748	0.96	0.76													42,335	6.09
R2544	G045.6		758	1.60	1,286	0	0		−	−		−	−		−	−		−	−	43,135	6.09
R2545			113*	1.14*	147	0	0		−	−		−	−		−	−		−	−	40,768	6.35
R2546			312*	0.55*	157	1.13*	0			−			−			−			−	41,351	6.35
R2547			355*	0.75*	247	1.08*	0.84													41,237	6.38
R2548			149*	1.47	198	0.83*	0.51													40,648	6.38
R2551			176*	1.70	266	2.31	2.22		+	+										36,248	6.33
R2552			0	0	0	218	134		+	+		+	+		+	+		+	+	35,095	6.35
R2553			0	174*	0	131	207*	+	+	+	+	+	+	+	+	+	+	+	+	36,817	6.29
R2554			326	0.93	519	1.18	0.80*													39,657	6.30
R2555			181	1.02	229	0	0		−	−		−	−		−	−		−	−	41,689	6.58
R2556			640	1.40	401	0.88	0.71													41,237	6.61
R2557			635	0.50*	856	0	0.16*	−	−	−		−	−		−	−		−		44,920	6.45
R2559	G059.4		2,583	1.50	3,454	1.53	1.65													51,685	6.13
R2560	G054.6		683	0.80*	807	0.31	0.21*		−	−		−	−							51,138	6.15
R2561	G058.5		202	1.36	226	0.42	0.29		−	−			−							50,639	6.17
R2564			30*	5.6*	NR	193*	175*	+			+			+						57,000	6.00
R2565			213*	1.18	107	3.06	3.48		+	+		+	+							58,356	6.13
R2566			353	1.56*	369	0.99*	0.99													53,654	6.05
R2567			0	0	342	0.78	0.55													53,907	5.93
R2570			70	1.12*	107	0.84	0.51*													63,314	6.16
R2571			90	1.73	282	0.36	0.30		−	−			−							66,701	6.27
R2572			1,866	1.34	1,995	0.78	0.55*													49,142	5.81
R2573			742	1.21	613	1.33	1.04													49,142	5.72
R2574			268	0.95	366	0	0		−	−		−	−		−	−		−	−	54,714	5.77
R2575			197*	2.45*	0	5,163	4,674	+	+	+		+	+		+	+		+	+	47,613	5.65
R2576	F050.3	*sucB*	1,290	0.49	2,071	0.41	0.57	−	−											47,400	5.73
R2578			151	1.41*	212	0	0		−	−		−	−		−	−		−	−	46,592	5.83
R2581			237	3.30*	363*	1.23*	1.88*	+			+									52,078	5.51
R2582			319*	2.84*	441*	1.00*	0.72*	+												53,654	5.46
R2584			278	1.47	310	0	0		−	−		−	−		−	−		−	−	19,458	6.50
R2585	H013.2		667	1.15	940	0.91	0.51													15,346	6.53
R2586			129	3.12*	247	4.45	4.08	+	+	+	+	+	+							14,190	6.49
R2587			0	0	225*	1.91*	2.02*			+										16,390	6.52
R2588			34*	4.68*	0	150	97	+	+	+	+	+	+		+	+		+	+	38,206	6.87
R2590			176*	1.79	331	0	0		−	−		−	−		−	−		−	−	37,518	6.42
R2592			283*	0.82	487	0.47	0.24		−	−			−							26,869	6.95
R2593			634	1.04	698	0.84*	0.90*													22,805	7.14
R2596			301*	0.85	301	0	0		−	−		−	−		−	−		−	−	27,559	6.78
R2597			236	1.68*	866	0	0		−	−		−	−		−	−		−	−	25,712	6.68
R2598			145*	2.19	0	181	202*	+	+	+		+	+		+	+		+	+	25,517	6.64
R2600			704*	0.46*	783	0	0	−	−	−		−	−		−	−		−	−	32,343	6.38
R2601			188*	NR	313	0.27	0		−	−		−	−			−			−	28,535	6.33
R2607			270	2.87*	221	5.12	6.18*	+	+	+		+	+		+	+				11,143	7.10
R2608			76*	0.85*	597*	0*	0*		−	−		−	−		−	−		−	−	21,520	6.62
R2609			67	0	433	0.25	0	−	−	−	−	−	−	−		−	−		−	21,536	6.72
R2610			32*	4.03*	0	233	243*	+	+	+	+	+	+		+	+		+	+	21,771	6.39
R2611					0	81*	0		+			+			+			+		21,733	6.42
R2612			773	3.42*	1,038	3.75	3.67	+	+	+	+	+	+							19,967	6.72
R2613			268*	0.79*	240	0.45	1.27*		−											19,216	6.73
R2615			143*	4.54	291*	2.63*	3.42*	+	+	+	+		+							14,707	6.87
R2616			809	1.43	846	0.44	0.34		−	−										17,151	7.19
R2617			359*	1.22	217*	1.36*	1.07*													17,151	6.95
R2619			163*	2.60#	367	0.48	0.42*	+	−	−										20,223	6.87
R2620			172	2.49*	227	2.18	1.17	+	+											20,098	6.95
R2621			724*	1.31	976	0.70	0.28			−			−							16,214	4.56
R2622			168	0.61	262	0	0		−	−		−	−		−	−		−	−	16,335	4.65

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TABLE 3—*Continued*

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f]												MW[g]	pI
								2-fold			3-fold			5-fold			10-fold				
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R2623	AO19.0	*fldA*	86*	3.18*	140	1.89	1.45*	+			+									21,200	4.65
R2624			61	1.42*	121	0.90	0.61*													21,615	4.59
R2627			681	0.18*	134*	1.69*	0.77*	−			−			−						21,536	4.27
R2628			238*	0.67*	114	3.28*	2.11*		+	+		+								21,661	4.35
R2630	E061.0		282	1.08*	221*	1.22*	0.76*													53,408	5.62
R2632			234	2.74*	263	1.36	0.67	+												50,482	5.65
R2634			536	1.03	464	0.30	0.16		−	−		−	−			−				55,293	5.49
R2636			235*	1.20*	104*	1.93*	1.63*													126,505	5.75
R2638			289	0.88	227	0.79	0.79													59,988	5.88
R2639	G074.0	*pfl*	3,590	0.36	3,355	0	0	−	−	−		−	−		−	−		−	−	103,034	6.02
R2640			1,706	0.73	1,278	2.93	3.58		+	+			+							97,490	5.99
R2642			366*	1.29*	267*	2.88*	3.01*		+	+			+							96,177	6.06
R2643			1,096	0.49*	4,016	0.06	0.09	−	−	−		−	−		−	−		−	−	101,603	6.05
R2644			1,511	0.71*	1,664	0	0		−	−		−	−		−	−		−	−	101,603	5.94
R2646			818	0.69*	219*	1.00*	1.00*													117,345	5.95
R2647			453	1.11*	161*	5.95*	3.00*		+	+		+	+		+					81,506	6.19
R2648			0	69*	0	125	146	+	+	+	+	+	+	+	+	+	+	+	+	71,372	6.04
R2649			75*	3.03	91	5.08	3.59	+	+	+	+	+	+		+					72,109	5.91
R2650			176	0.89	205	0.53	0.44			−										76,075	5.82
R2651			0	84	0	87.00	79.00	+	+	+	+	+	+	+	+	+	+	+	+	72,864	5.84
R2654			712*	0.42*	365*	0.79*	1.09*	−												104,495	6.57
R2655			689	0.97	1,051*	3.74*	2.89*		+	+		+								113,932	6.58
R2660			0	0	145	0.51*	0.76													45,847	6.05
R2661			570*	0.94*	315*	1.30*	0.70*													45,143	6.08
R2664			187	1.78	349	2.40	1.31*		+											34,805	6.62
R2665			36*	3.33*	110*	1.61*	1.54*	+			+									35,240	5.89
R2666			1,641	0.94	1,424	1.46	1.18													23,584	5.79
R2668			0	273*	0	987	395	+	+	+	+	+	+	+	+	+	+	+	+	29,306	7.27
R2669			292	3.07#	763	0	0	+	−	−	+	−	−		−	−		−	−	49,142	5.59
R2670			528*	0.00	541	0.43*	0.41	−	−	−	−			−			−			50,482	5.46
R2671	C074.0		218*	1.49*	205	2.27	4.75		+	+			+							80,547	5.32
R2672	C075.0		227	3.41*	312	1.17	1.55	+			+									81,506	5.42
R2678			383*	0.45	288*	1.05*	1.49*	−												47,303	5.56
R2685	F038.5	*rimL*	491*	2.35*	1,365	1.07	0.77	+												39,753	5.76
R2710			0	543*	0	873*	0	+	+		+	+		+	+		+	+		16,093	5.59
R2712			423*	1.19*	249*	7.40*	9.30*		+	+		+	+		+	+				9,714	5.21
R2716			46*	6.61	206	1.28	1.30	+			+			+						21,580	7.54
R2720			2,431*	0.52*	1,260	0.99*	1.00*													23,784	5.69
R2721			555	0.95	552	1.94	1.17													42,439	5.30
R2722			0	184*	0	263	193*	+	+	+	+	+	+	+	+	+	+	+	+	22,364	5.64
R2724	B027.0		0	273	0	463	492	+	+	+	+	+	+	+	+	+	+	+	+	24,144	5.18
R2725			90*	2.95*	0	212	182	+	+	+		+	+		+	+		+	+	47,613	5.07
R2726			232*	1.13*	253	1.31	1.24													43,953	5.24
R2727			423	1.07*	220*	3.56*	2.07*		+	+		+								51,138	5.28
R2728	B040.5		0	215*	0	650	848	+	+	+	+	+	+	+	+	+	+	+	+	40,648	5.09
R2729			104*	4.09	0	411	558	+	+	+	+	+	+		+	+		+	+	46,388	6.00
R2730			0	0	0	438	461		+	+		+	+		+	+		+	+	52,283	6.24
R2731			1,187*	0.71*	803	1.69	0.80													43,779	6.08
R2733	H054.5	*trpD*	397	0.84*	NR	0	0													51,878	6.39
R2736			438	0.69	723*	1.18*	1.11*													46,730	5.47
R2737			1,682*	0.17	560*	0	0	−	−	−	−	−	−	−	−	−		−	−	49,632	5.38
R2746			44*	5.57*	0	510*	400	+	+	+	+	+	+	+	+	+		+	+	21,709	4.33
R2747			0	57*	0	88*	65	+	+	+	+	+	+	+	+	+	+	+	+	22,852	4.53
R2754			0	1,092	0	328*	85	+	+	+	+	+	+	+	+	+	+	+	+	14,190	6.44
R2755			0	0	0	208*	171		+	+		+	+		+	+		+	+	8,700	6.55
R2756			105*	1.12*	176	1.00*	0.93*													10,092	7.26
R2757			187*	0.46*	415*	0.52*	0.54*	−												19,047	6.65
R2765			180*	1.09*	0	396*	401		+	+		+	+		+	+		+	+	38,610	6.05
R2779			155	1.00*	0	1,278*	1,598		+	+		+	+		+	+		+	+	8,900	5.81
R2780			0	0	0	0	235			+			+			+			+	14,319	6.95
R2782			0	195*	0	0	111*	+		+	+		+	+		+	+		+	27,095	6.64
R2784			316*	0.98	0	0	199*			+			+			+			+	23,335	5.05
R2786			224	1.13*	0	387*	273*		+	+		+	+		+	+		+	+	29,569	5.46
R2787			138	1.12	147	0	0		−	−		−	−		−	−		−	−	53,654	6.30

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TABLE 3—*Continued*

Protein RRM[a]	A-N[b]	Gene[c]	ppm PE[d]	Ratio PHN[e]	ppm PW[d]	Ratio PLE[e]	Ratio PLL[e]	Induction of protein[f] 2-fold			3-fold			5-fold			10-fold			MW[g]	pI
								PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL	PHN	PLE	PLL		
R2788			321	0.60	230	0	0		−	−		−	−		−	−		−	−	49,764	6.39
R2789			0	0	0	0	461*			+			+			+			+	48,703	5.74
R2800			267*	0.74*	0	0	0													30,105	5.61
R2802			223	1.14	216*	0	0		−	−		−	−		−	−		−	−	45,571	6.00
R2804			624*	0.76	567	0	0		−	−		−	−		−	−		−	−	49,380	5.92
R2807	E133.0	*carB*	1,426	1.04	3,051	0	0		−	−		−	−		−	−		−	−	127,208	5.49
R2808			57	3.76*	80*	7.98*	7.54*	+	+	+	+	+	+		+	+				9,908	4.42
R2810			0	0.00	714	0	0		−	−		−	−		−	−		−	−	20,510	6.76
R2812			157*	1.06*	765*	0	0		−	−		−	−		−	−		−	−	24,963	6.71
R2818			403*	1.07*	0	0	0													24,220	5.11
R2821			173*	1.54	0	0	0													47,155	5.09
R2824			174*	0.56*	0	0	0													50,967	5.58
R2828			93*	1.32	0	0	0													68,602	5.64
R2830			256*	1.07*	0	0	0													35,240	5.23
R2831	B046.5		0	199	0	0	0	+			+			+			+			45,710	5.12
R2832			0	241	0	236*	204*	+	+	+	+	+	+	+	+	+	+	+	+	59,563	5.94
R2899			1,372	0.62*	0	0	0													34,660	4.89
R2909			82*	1.02*	0	0	0													12,042	5.30
R2932	B024.6		0	241	0	0	0	+			+			+			+			22,331	5.10
R2941			188	3.03*	0	0	0	+			+									23,277	6.02
R2951			357	0.82*	0	0	0													93,635	5.30
R2972	G028.1	*araD*	57*	1.96*	0	0	0													29,165	6.06
R2973	G029.3	*thyA*	163*	1.62*	0	0	0													28,285	6.00
R2979			389*	0.67*	0	0	0													49,899	6.01
R2983			2,127	1.92	0	0	0													45,069	5.32
R2992			63	11.62*	0	0	0	+			+			+			+			8,400	4.88
R2993			87*	2.72*	0	1,260	1,397	+	+	+		+	+		+	+		+	+	7,000	5.10
R3004			408	1.63*	0	0	0													11,248	6.60
R3010			0	277	0	0	0	+			+			+			+			22,470	6.01
R3019			199	2.30	0	483*	951*	+	+	+		+	+		+	+		+	+	35,385	4.96
R3023			0	300	0	0	0	+			+			+			+			36,248	5.38
R3024			0	3,099*	0	1,042*	0	+	+		+	+		+	+		+	+		37,239	5.47
R3027			0	388	0	0	0	+			+			+			+			40,648	5.46
R3029			192*	22.00	0	0	0	+			+			+			+			42,439	5.20
R3030			0	416	0	0	0	+			+			+			+			42,335	5.16
R3035			0	718*	0	0	0	+			+			+			+			23,584	6.60
R3036			99*	4.52*	0	0	0	+			+									23,277	6.61
R3040			0	2,896	0	0	0	+			+			+			+			44,039	6.33
R3041			0	264	0	0	0	+			+			+			+			43,953	6.38
R3042			0	355*	0	0	0	+			+			+			+			44,124	6.26
R3058			71	2.46*	89	5.11	6.40	+	+	+		+	+		+	+				6,500	4.63
R3059			0	105	0	0	0	+			+			+			+			54,714	4.85
R3065			0	304	0	0	0	+			+			+			+			41,237	5.56
R3067			275	2.28*	0	0	0	+												50,000	5.59
R3079			258	0	0	0	0	−			−			−			−			37,000	5.14
R3085			482	0	0	0	0	−			−			−			−			103,034	5.59
R3306			0	553*	0	1,021*	933*	+	+	+	+	+	+	+	+	+	+	+	+	8,200	5.35
R3307			389	1.33	602	1.81	1.51													9,614	4.92

[a] Each protein has a unique name based on the RRM.
[b] A-N, The alpha-numeric designation used in the gene-protein database (34, 45) and referenced in the Swiss-Prot (2) and ECD (14) databases.
[c] Gene name for the protein (see reference 46).
[d] ppm, ppm value for each protein under phosphate excess conditions (see Materials and Methods). An asterisk indicates that the SE was ≥20% of the mean; a number symbol (#) indicates that the induction of the protein could not be visually verified; NM, no protein match; NR, data not reproducible.
[e] The ratio of the ppm value for the P-restrictive condition indicated (PHN, PLE, or PLL) to the ppm value in P_i excess for that protein (relative differential rate of synthesis as described in Materials and Methods). See footnote *d* for the definitions of * and #.
[f] The ratio for a protein is greater (+) or less (−) than 2-, 3-, 5-, or 10-fold.
[g] MW, approximate molecular weight of the protein based on the migration of the gels (46).

(K_2HPO_4) or PHN were determined from growth curves of the two strains of interest. As shown in Fig. 1A, when *E. coli* W3110 is grown in medium containing an initial P_i concentration of 1.32 mM (ample P_i), logarithmic growth continued until the OD_{600} of the culture approached 1.0. An initial P_i concentration of 0.066 mM resulted in the cells doubling at the same rate as that in the culture with ample P_i until the P_i was depleted (about OD_{600} of 0.35). Concomitant with a change in the growth rate was a dramatic increase in the alkaline phosphatase activity, an indication of PHO regulon gene expression. Like other laboratory strains of *E. coli* K-12, W3110 is unable to utilize phosphonates as the sole phosphate source, because of the cryptic nature of the *phn* (EcoK) locus (51). An isogenic Phn$^+$ derivative of W3110, EP820, was isolated as described in Materials and Methods, and its growth rate was determined in medium containing either P_i or phosphonate (Fig. 1B). The growth rate in phosphonate-containing medium is only 42% of that in P_i-containing medium. The addition of P_i to the culture growing in phosphonate resulted in a rapid shift to a growth rate matching that of the P_i culture, demonstrating that the difference in growth rate between the two cultures was due to the P source (data not shown).

Synthesis rates of proteins during growth on PHN and P limitation. We examined the pattern of proteins synthesized under the three growth conditions described in the previous section. Duplicate cultures of each strain were grown and labeled for each experimental condition. Two gels of each sample were run. The ppm values for each protein were determined as described in Materials and Methods.

Table 3 includes data on all 816 proteins detected in this study. Each protein has a unique name (RRM) and many have been cross-referenced (by the alpha-numeric [A-N] name) to proteins previously reported in the *E. coli* gene-protein database (46). For proteins that have previously been determined to be the product of a certain gene, the gene names are included in Table 3. For the samples prepared from cultures with ample phosphate (PW and PE), the ppm value for each protein is given. For the samples grown in P limitation (PLE and PLL) and on PHN, the relative differential rate of synthesis of each protein is given (see Materials and Methods for the calculation of the relative differential rate of synthesis). The proteins for which synthesis was induced or repressed are indicated. Additional figures and tables are presented to aid in the analysis of this large data set.

This study included 20 2-D gels; only three images are presented. Figure 2A is a representative image of cultures grown in excess P_i (PW), Fig. 2C is one of the images from the PLE samples, and Fig. 2E is the image of a sample grown on PHN. The first two images display the degree of translational reprogramming that occurred upon P limitation. For example, in the lower right corner of the gel are the ribosomal proteins L7 and L12. In Fig. 2A these are abundant proteins. In the P limitation image (Fig. 2C), L12 is not detectable and L7 is significantly repressed relative to the control (Fig. 2A). Synthetic images were generated to display the locations of the proteins with a twofold or greater change in synthesis rates (Fig. 2B and D). The locations of all of the proteins (as *x* and *y* coordinants) are available in the electronic form of the database, ECO2DBASE (see Materials and Methods for electronic submission of data). Figure 2A displays all of the proteins whose synthesis is repressed twofold or more, and Fig. 2D displays those induced twofold or more. The synthetic image in Fig. 2B can be overlayed onto Fig. 2A, and Fig. 2D can be overlayed on Fig. 2C to ascertain the names of the proteins given in Table 3.

Identifying members of the PL and PHN stimulons. In Fig. 3 the proteins are grouped by the magnitude of their fold change between ample phosphate and P limitation or growth on PHN. All three experimental conditions are displayed so that comparisons among these conditions can be made. The histogram reveals some major differences between P limitation and growth on PHN. In the experiment for growth on PHN, far fewer proteins were repressed than in the P limitation experiment. About half of the proteins maintain the same rate of synthesis during growth in P_i compared with that on PHN. The histogram also reveals the high degree of similarity between the early and late P limitation samples.

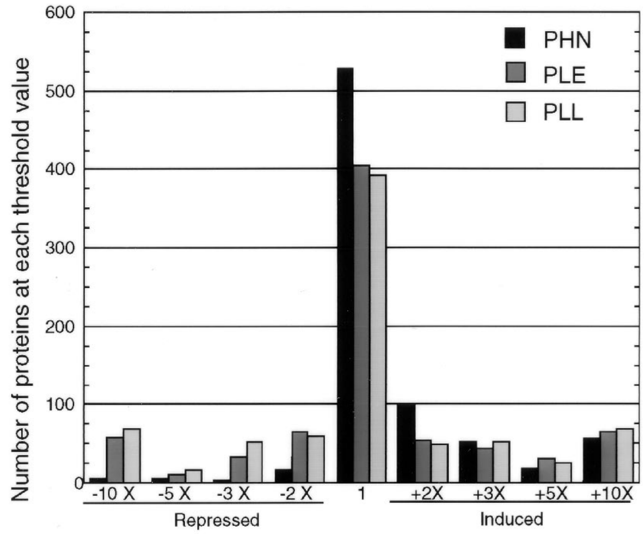

FIG. 3. Histogram showing the number of proteins whose relative differential rates of synthesis were induced (+) and repressed (−) two-, three-, five-, and 10-fold in PHN-containing versus P_i-containing media (solid bars) and during early P limitation (dark gray bars) and late P limitation (light gray bars) compared with under ample P_i conditions.

Although the histogram presented in Fig. 3 is useful for finding trends in the translational reprogramming that occurred during growth under different conditions, it does not allow for tracking the responses of individual proteins. For example, from the histogram we can conclude that there are about 60 proteins induced 10-fold or more by both P limitation (both early and late) and growth on PHN, but this graph does not reveal whether these are the same proteins. These questions can be addressed by highlighting different sets of proteins in distributions of each data set.

Figure 4 displays the distribution of the data from each experiment. Each distribution is repeated six times, with a different set of proteins highlighted in each. These distributions allow one to see how, for example, proteins that are induced early in P limitation behave later. Similarly, it can be seen that many proteins induced in PLE are not induced in PHN but rather are unchanged (or repressed). A comparison between nitrogen starvation (data from ECO2DBASE, see Materials and Methods) and P limitation revealed even less overlap among the proteins with induced synthesis. This finding indicates that P limitation and growth on PHN are more similar to each other than the responses to P limitation and nitrogen starvation are to each other.

Identifying putative members of the PHO regulon. Since the synthesis of most of the known proteins of the PHO regulon are dramatically induced during both P limitation and growth on PHN, we expected to see a greater overlap between these conditions for those proteins with high induction ratios. The Venn diagrams in Fig. 5 show the number of proteins whose synthesis is induced or repressed by these conditions with threshold values of 2-fold or more (Fig. 5A and C) or 10-fold or more (Fig. 5B and D). What is striking from this presentation is that the percentage of overlap for induced proteins (about 50%) is the same regardless of the threshold value used. A significant overlap was also seen with respect to the proteins repressed twofold or more; 50% of these proteins are also repressed by P limitation.

We attempted to match proteins that are known to be members of the PHO regulon to proteins induced in these experi-

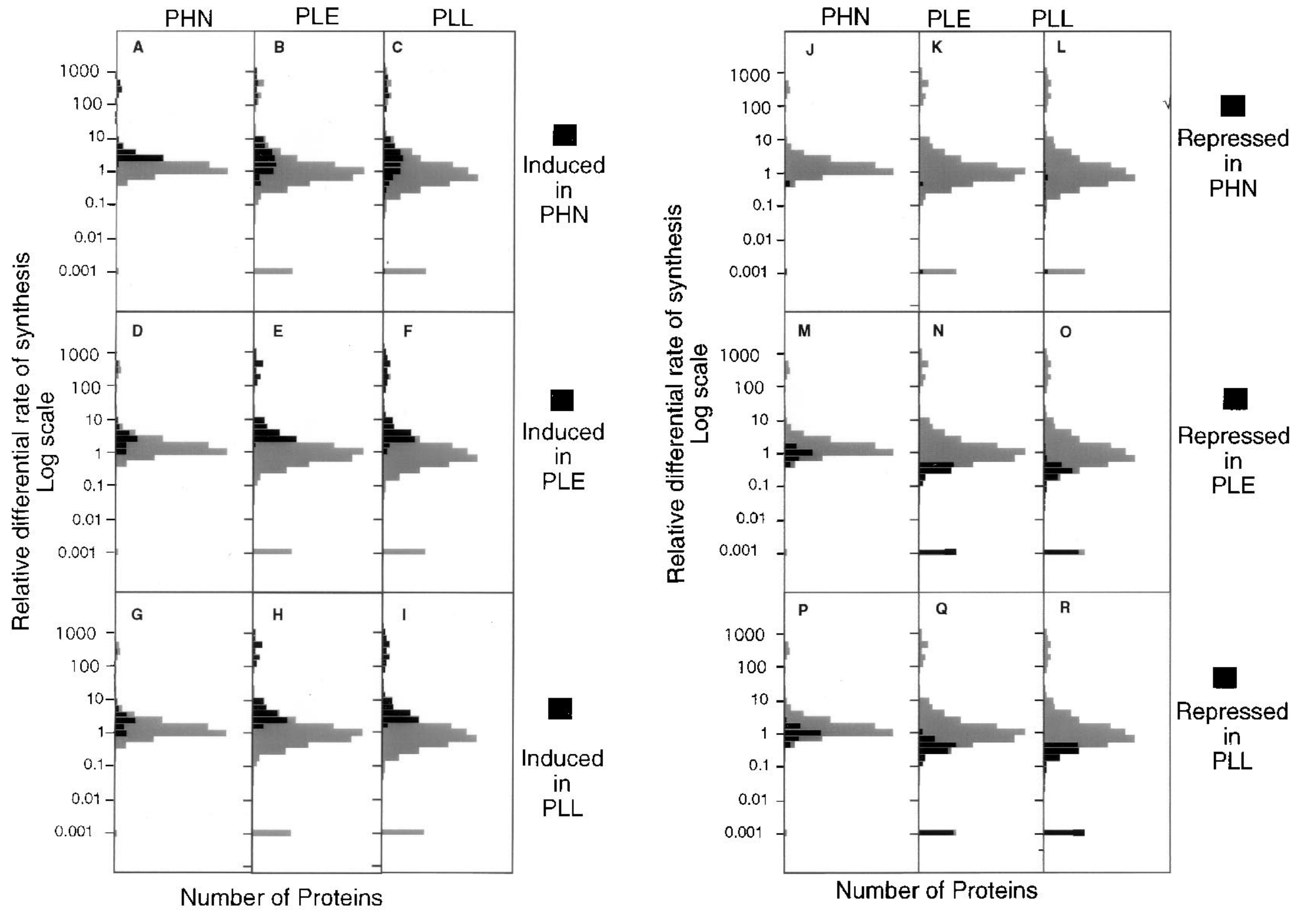

FIG. 4. Tracking sets of proteins induced or repressed in different P conditions. In order to compare the responses of sets of proteins under different conditions, the distributions of the ratios for PLE, PLL, and PHN samples are shown. Each distribution is repeated six times (vertically). In each row of panels a different protein response group is indicated by solid areas as follows: proteins induced twofold or more by growth in PHN (A to C), proteins induced during P limitation early (D to F), proteins induced during P limitation late (G to I), and proteins repressed twofold or more in the three experiments in the same order in which the induced proteins were presented (J to R) (A, D, G, J, M, and P) PHN distribution (mode height of 528 proteins); (B, E, H, K, N, and Q) PLE distribution (mode height of 405 proteins); (C, F, I, L, O, and R) PLL distribution (mode height of 391 proteins).

ments. Using information, relating the pIs and molecular weights of proteins to their migration on 2-D gels (46), we are able to predict the locations of the gene products. This was done for the PHO regulon members and a few other proteins known to be induced by P limitation whose pIs were less than 7 (proteins with pIs greater than 7 cannot be resolved on these gels). The predicted positions on the 2-D gel were noted on the synthetic image (Fig. 2D). Most were close in proximity to proteins observed in this study.

Several previously identified proteins were among the proteins whose synthesis responded to P limitation and/or growth on PHN. We examined the promoter regions of genes encoding proteins identified in this study as being induced or repressed twofold or more by phosphate restriction. For 11 of these genes, a sequence similar to that of a *pho* box (Fig. 6) was seen. Not all of these spanned the −35 region, although all but one were positioned near the −35 region. Eight of them had spacing between the 7-bp repeats different from that in the nine promoters known to be regulated by PhoB. Three of the 11 genes encoded proteins that were repressed rather than induced by P limitation and growth on PHN.

Protein synthetic capacity involved in the translational reprogramming during P limitation and growth on PHN. A global analysis also allows one to examine the amount of the

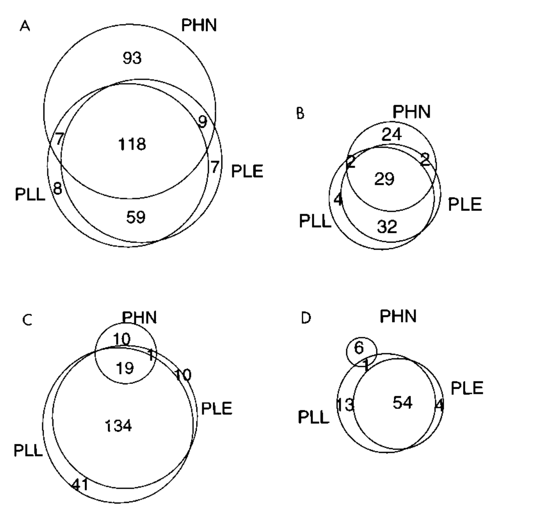

FIG. 5. Venn diagrams showing the overlap between the PHN and PL stimulons. The overlap of proteins either induced twofold or more (A) and 10-fold or more (B) or repressed twofold or more (C) and 10-fold (D) are shown. Each circle has a radius proportional to the total number of proteins induced. The numbers indicate the number of proteins which overlap in each segment.

Consensus	C	T	T G	T	C	A	T	ATAT A A	C	T	T G	T	C A	A	C T	# to -10	*gene name*	Response
Freq. (of 10)	7	9	9	9	7	9	9	6,8,7,8	7	10	10	9	10	10	10	10		
	C	**T**	**T**	A	**C**	**A**	C	TTTT	G	**T**	**T**	**T**	**C**	**A**	**C**	15	*amn* (17)	+
	C	**T**	**T**	G	**C**	G	**T**	GAAAAA	**C**	**T**	**G**	**T**	**C**	C	G		*eda* (6)	+
	C	**T**	**G**	**T**	T	T	G	TTTTT	G	**T**	**T**	**T**	**C**	**A**	**T**	119	*folA* (40)	+
	C	**T**	**T**	**T**	A	**A**	**T**	AAGTA	**C**	**T**	**T**	**T**	G	T	A	-2	*gnd* (26)	+
CTTACATtc	**C**	**T**	**G**	C	T	**A**	**T**	TGCACAA	**C**	**T**	**G**	A	**A**	T	**T**	9	*hns* (7)	+
	C	**T**	**T**	**T**	G	C	C	CTG	**C**	G	**T**	G	**C**	T	**T**		*ilvA* (15)	+
	A	**T**	**T**	**T**	**C**	T	**T**	CA	**C**	**T**	**T**	**T**	**C**	C	G	12	*pfkB* (5)	+
	C	**T**	**T**	**T**	A	T	G	CCCTT	G	**T**	**T**	C	G	**A**	**T**	8	*rimL* (43)	+
	C	**T**	**T**	**T**	G	T	A	GCA	C	**T**	**T**	**T**	C	A	**C**	25	*ompF* (12)	-
TTGACATact	G	G	G	**T**	**C**	**A**	**T**	TTAC	**C**	**T**	**G**	C	G	T	G	11	*pfl* (36)	-
	C	**T**	**G**	**T**	A	T	A	TT	**C**	A	**T**	**T**	**C**	**A**	G	11	*ssb* (1)	-
Freq. (of 11)	9	10	11	8	4	4	5		8	9	11	7	8	5	6			

FIG. 6. Putative PhoB boxes in the promoter regions preceding genes encoding proteins that are induced or repressed in PLE, PLL, and/or PHN samples. The consensus PhoB box (top line) is defined as two direct repeats spaced by four bases which are part of the −35 region of the promoters and end 10 bases upstream of the beginning of the −10 region of the promoter (20, 44, 52). The second line shows the frequency at which each of the bases in the consensus sequence are found among 10 promoters previously shown to be activated by PhoB (20). The next 11 lines show a region of the promoters for operons encoding proteins induced or repressed (indicated in the last column as + or −, respectively) in the present study. The last line shows the frequency at which the consensus bases were found among these 11 genes. The numbers in parentheses to the right of the gene names are the references for the sequence for the genes.

protein synthetic capacity that is subsumed in the proteins whose synthesis is induced or repressed. Because these samples were pulse-labeled, the data represent the radioactivity incorporated during the pulse, not the total protein mass. To determine how much of the synthetic capacity (during the pulse-label) was consumed by proteins whose synthesis was induced, repressed, or unchanged under the PHN or P limitation conditions compared with the ppm values during the P_i-excess conditions, the sum of the ppm values for the proteins in each category was determined. The ppm values for PHN, PLE, and PLL are not given in Table 3, only the ratio is given, but the ppm value for each protein is its ppm value in the P_i-excess condition times the ratio. These results are presented as pie graphs (Fig. 7). Comparisons are made between (i) the PE and PHN samples, (ii) the PW and PLE samples, and (iii) the PW and PLL samples.

DISCUSSION

Twenty years have passed since O'Farrell published his method of 2-D gel electrophoresis which separates proteins on the basis of two independent parameters (32). Although it was quickly recognized as a potentially powerful tool for global quantitative studies of levels and synthesis rates of proteins, very few of these studies have been published (e.g., see reference 34) largely because the detection and quantitation tools were not sufficiently developed to monitor 1,000 proteins whose levels of synthesis vary in abundance over a fivefold dynamic range. Two recent developments have changed the situation. First, the development of PhosphorImaging systems has enhanced the ability to detect radiolabeled proteins (33); and second, continued improvements in image analysis systems (both the processing speed of computers and improvements in software) have decreased the time required to find, quantify, and match proteins on 2-D gels. This report is the first contribution to the *E. coli* 2-D gel database (gene-protein database) with computer-aided image analysis to complete a global study of the changes in synthesis rates of proteins in response to an environmental stress.

In the early 1980s we recognized P limitation in *E. coli* as a good choice to test tools available to perform global studies via 2-D gels because it was the largest stimulon identified by reductionist approaches and because one regulon (PHO) induced by the condition was well-characterized. This report is our third attempt in the past 15 years at a global study of this condition. The first study focused on finding overlaps among three stimulons imposed by different nutrient starvation conditions (47). The results of these studies were also in agreement with results obtained by *lacZ* fusions that showed that certain phosphate starvation-inducible (PSI) promoters are inducible only by P limitation while other PSI promoters are inducible by other nutrient starvations as well (54). Another report also found overlaps among the proteins synthesized at higher rates in response to nutrient starvations (9). The second study focused on identifying regulons within a stimulon (35). This third study has focused on distinguishing between proteins involved in adapting the cells to utilize alternative P sources and the proteins involved in preparing the cells to survive stationary phase brought on by P depletion.

In the present study we examined two P-restrictive condi-

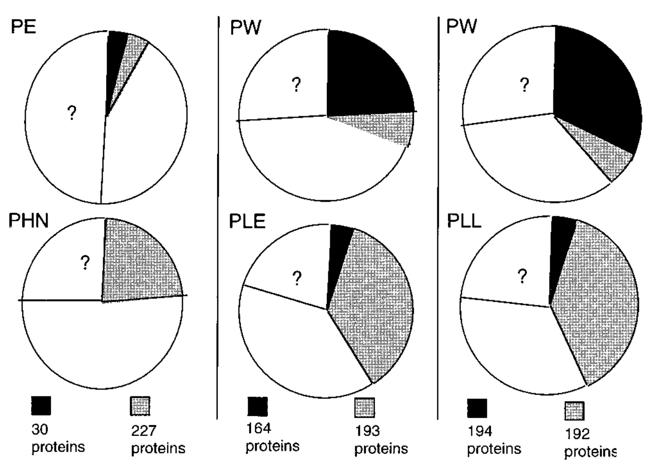

FIG. 7. Fraction of cellular protein mass responding to P limitation or growth in PHN. The charts represent the total radioactivity incorporated (10^6 cpm loaded on 2-D gel; 1 cpm = 1 ppm) for each conditions. For each pair of pie graphs the same proteins are represented by the shaded sections, and the size of each section reflects the sum of the ppm values for that group of proteins (induced [ ] unchanged [□] or repressed [■]). ?, not detected in this study.

tions: P limitation, a nongrowth condition due to the depletion of P_i with no other P source, and growth with phosphonate as the sole P source, a slow growth condition due to a restriction in the supply of P to the cells (16). Proteins involved in the adaptation of cells to insufficient P_i and to alternative P sources are expected to respond similarly in the two conditions; proteins whose levels are altered to prepare cells for survival in stationary phase may respond differently. Whether the changes in synthesis of these proteins are being controlled actively (genes controlled transcriptionally by other cellular molecules) versus passively (genes whose promoters remain open during these conditions) cannot be distinguished from these experiments. Passive control of growth rate-controlled genes in media with different compositions has been described previously (19).

In summary, we were able to detect 816 proteins under one or more of the growth conditions. Only about 400 proteins had the same rates of synthesis during P limitation and during growth in abundant P_i. During growth on PHN, 528 proteins maintained the same differential rate of synthesis (less than twofold variation) as that during growth in ample P_i. All proteins with differential rates of synthesis greater than 2.0 (called induced proteins) or less than 0.5 (called repressed proteins) were classified as being in a stimulon. We found 193 induced and 164 repressed proteins in the PL (early) stimulon, 192 induced and 194 repressed in the PL (late) stimulon, and 227 induced and 30 repressed proteins in the PHN stimulon. The early and late PL stimulons contained almost the same proteins (177 induced and 153 repressed) and are collectively called the PL stimulon (208 induced and 205 repressed). The PL and PHN stimulons shared 118 induced and 19 repressed proteins.

Because the amount of radioactivity for each protein was obtained as a fraction of the total protein radioactivity (ppm), it was possible to add-up the ppm for proteins that were induced or repressed to obtain a measurement of synthetic capacity (during the pulse-label) consumed in the response. About 40% of the total synthetic capacity was consumed by the 400 proteins responding during P limitation conditions, and about 30% of the synthetic capacity of cultures grown on PHN was associated with the 257 responding proteins (Fig. 7).

Our findings permit several conclusions about the cells' responses to P limitation and growth on PHN.

(i) Responses to stress involve a large number of proteins and a significant portion of the cell's protein-synthesizing capacity. On the basis of the assumption that the *E. coli* chromosome contains roughly 4,000 genes encoding proteins, 10% of the genes respond to P limitation and 6% respond to growth on PHN. Since this is only one of the many stress conditions *E. coli* encounters, we predict that many of these responders will also be members of other stimulons.

(ii) The adaptive response results primarily in the induced synthesis of proteins. As stated previously, the adaptive response to P restriction should be represented among the proteins whose synthesis was induced or repressed by both P limitation and growth on PHN. We found 118 induced protein but only 19 repressed proteins responding to both conditions (Fig. 5), suggesting that the adaptive response primarily involves enhancement of the synthesis of selected proteins. As shown in Fig. 3, the total number of proteins induced by P limitation is very similar to the total number induced by growth on PHN. Similarly, a large portion of the cell's protein synthetic capacity is diverted to proteins with rates of synthesis that are twofold or more higher for growth on PHN than for growth in ample P_i (Fig. 7). These findings were somewhat surprising given that cells grown on PHN must balance their adaptive response with the need for other basic growth functions. The P limitation cells are entering stationary phase and probably have a sufficient quantity of the protein required for basic growth functions; they might be expected, therefore, to be able to channel much more of their protein synthetic capacity into adaptive and survival responses.

(iii) The adaptation to stationary phase involves primarily repression of proteins. The proteins whose synthesis is adjusted to prepare cells to survive stationary phase should be among the proteins responding to P limitation but not to growth on PHN. Since P limitation resulted in the repression of 205 proteins compared with only 30 for growth on PHN, the survival response clearly involves repression of many proteins as a dominant feature. Comparison of survival responses to other conditions will eventually reveal which proteins are important for survival in specific environments and which are involved in the more general switch to stationary phase of growth. For example, many of the proteins repressed by P limitation are also repressed by nitrogen starvation (45), even though there was very little overlap between the proteins induced by these two conditions. Therefore, these proteins may not all be specific to P limitation but to a more general programming to stationary phase of growth.

(iv) The PHO regulon could be as large as 137 proteins, 118 induced and 19 repressed, and may include well-characterized proteins not previously implicated as part of this regulon. From the analysis of the PL and PHN stimulons, we found 137 responding proteins in common (Fig. 5). This number represents 50% of the proteins induced by each condition and two-thirds of the proteins repressed by growth on PHN. These are all candidates for membership in the PHO regulon. Most of the known PHO regulon members can be tentatively recognized as proteins shown to be induced in these studies (Fig. 2E). Several identified responders were found to contain a sequence in their promoter region similar to the sequence called the *phoB* box (Fig. 6), suggesting that PhoB may regulate the expression of some well-characterized genes not previously suspected to be part of that regulon. The proportion of proteins in the overlap was about the same regardless of whether 2- or 10-fold was used as the threshold value. If these are members of the PHO regulon, it suggests that not all of the members have high induction ratios observed for known promoters of the regulon (52). Additional studies of *phoB* and *phoR* mutants will help in defining these proteins as PHO regulon members.

(v) The new pattern of protein synthesis upon P limitation is constant during the first hour. The differential rates of synthesis of most proteins at the two time points following depletion of P_i, 10 to 30 min (PLE) and 30 to 60 min (PLL), were nearly identical (Fig. 4). Other stress conditions, such as heat shock and treatment with hydrogen peroxide, have yielded transitory and sequential sets of proteins which are induced and repressed within this time frame (48).

(vi) The rates of synthesis of proteins belonging to a regulon can be differentially regulated under different stimuli. The heat shock proteins (regulated by sigma-32 [30]) are often referred to as general stress proteins (18), and yet only some were induced by P limitation (a stress condition). The heat shock genes *mopA*, *dnaK*, *grpE*, *ibpB*, and *htpG* are among the genes most highly induced during heat shock, but the synthesis of their corresponding proteins are not induced during P restriction, whereas other heat shock genes (*htpH*, *htpK*, *clpB*, and *mopB*) were induced. It was not determined if the induction of the subset of heat shock genes induced by P limitation is dependent on sigma-32. It has previously been reported that stress conditions (e.g., oxidative stress, treatment with heavy metal, and treatment with DNA damaging agents) other than heat shock usually induce only a subset of the regulon (48). Uncovering the regulatory system used to control the subset of heat shock proteins induced during P limitation could be enlightening for the study of P restriction and other stress conditions that induce subsets of the more general stress proteins.

From the analysis of these two stimulons, we classified the proteins belonging to both stimulons as being part of the adaptive response to P restriction and the proteins belonging to just the PL stimulon as being part of the adaptation to stationary phase of growth. However, the nearly 100 proteins whose synthesis was increased by growth on PHN but not P limitation have not been explained. Two possibilities are that (i) these might be involved specifically in the adaptation to growth on PHN (or maybe just this particular phosphonate) or (ii) they might be encoded by genes that are growth rate regulated (because the growth rate is much lower in media containing phosphonate than the growth rate in media containing P_i).

This global study of P restriction has contributed information on over 800 proteins. Although to date only about 100 of these proteins have been linked to their genes, the data annotated to each of these proteins will continue to grow as additional experiments are completed and the data are merged with this experimental set. Each protein should eventually be linked to its gene as work on the *E. coli* gene-protein database continues (28). Global studies of this type have contributed new information to those interested in detailed molecular and biochemical properties of single proteins, in signal transduction pathways for groups of coregulated proteins, and in the analysis of how an entire organism organizes and controls its entire complement of proteins.

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