

Functional Genomics of Plant Stress Tolerance (NSF DBI 98-13360)

Approaches towards defining Salt Stress Tolerance

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Abiotic stresses reduce plant productivity. We focus on gene expression analysis following the exposure of plants to high salinity, using salt-shock experiments to mimic stresses that affect hydration and ion homeostasis. The approach includes parallel molecular and molecular genetic experimentation.

- Comparative analysis is employed to identify functional isoforms and genetic orthologs of stress-regulated genes common to cyanobacteria, fungi, algae and higher plants.
- We analyze global gene expression profiles monitored under salt stress conditions through abundance profiles in several species: in the cyanobacterium *Synechocystis* PCC6803, in unicellular (*Saccharomyces cerevisiae*) and multicellular (*Aspergillus nidulans*) fungi, the eukaryotic alga *Dunaliella salina*, the halophytic land plant *Mesembryanthemum crystallinum*, the glycophytic *Oryza sativa* and the genetic model *Arabidopsis thaliana*.
- Expanding the gene count, stress brings about a significantly higher number of transcripts, compared to no-stress conditions, for which no function is known.
- We use microarray hybridizations to *Arabidopsis* (18,000 elements), *Mesembryanthemum* (~5,000 elements), rice (5,000 elements), corn (~5,000 elements), barley (~2,000 elements), selected *Synechocystis* PCC6803, and *Aspergillus nidulans* elements on microarrays, and a whole genome array of *Saccharomyces cerevisiae*.
- Also, we generate insertional mutants that affect stress tolerance in several organisms. More than 400,000 T-DNA tagged lines of *A. thaliana* have been generated, and lines with altered salt stress responses have been obtained.
- The integration of these approaches defines stress phenotypes, catalogs of transcripts, and a global representation of gene expression induced by salt stress. Determining evolutionary relationships among these genes, mutants and transcription profiles provides categories and gene clusters, which reveal ubiquitous cellular aspects of salinity tolerance and unique solutions in multicellular species.

Table 1: cDNA libraries for salinity stress-relevant ESTs.*Expressed as mM NaCl and length of stress treatment. For *D. salina*, molar concentrations of NaCl were used.

Name	Organism	Tissue	Stress*	Plant Age
AA	<i>A.thaliana</i> (Columbia)	Leaves	200; 20h	12w
AB	<i>A.thaliana</i> (Columbia)	Leaves	200; 3,6,9,12h	2-3w
AC	<i>A.thaliana</i> (Columbia)	Leaves & Roots	150; 20h	2-3w
AD	<i>A.thaliana</i> (Columbia)	Seedlings	Subtracted, 160 mM NaCl, 4h	10-14d
AF	<i>A.thaliana</i> (Columbia)	Roots	200; 6h	flowering
DA	<i>D. salina</i>	Cells	shift 1.7M & 2.5M to 3.4M; 5h	cell culture
HA	<i>H. vulgare</i> (Tokak)	Leaves	No Stress	~3w
HB	<i>H. vulgare</i> (Tokak)	Leaves	Drought ; 6 & 10h	~3w
HC	<i>H. vulgare</i> (Tokak)	Roots	Drought; 6 & 10h	~3w
HD	<i>H. vulgare</i> (Tokak)	Roots	No Stress	~3w
MA	<i>M. crystallinum</i>	Leaves	No Stress	5-6w
MB	<i>M. crystallinum</i>	Leaves	400; 30h	5-6w
MR	<i>M. crystallinum</i>	Leaves	400; 48h	5-6w
MC	<i>M. crystallinum</i>	Roots	No Stress	5-6w
ME	<i>M. crystallinum</i>	Roots	400; 6h	5-6w
MF	<i>M. crystallinum</i>	Roots	400; 12h	5-6w
MG	<i>M. crystallinum</i>	Roots	400; 30h	5-6w
MH	<i>M. crystallinum</i>	Roots	400; 78h	5-6w
MI	<i>M. crystallinum</i>	Seedlings	250; 3 d	14 d
MJ	<i>M. crystallinum</i>	2° Leaves	500; 5 d	8-9w
MK	<i>M. crystallinum</i>	1° Leaves	500; 6-7 d	6w
ML	<i>M. crystallinum</i>	Flowers & Seedpods	500; 6w	>12w
MM	<i>M. crystallinum</i>	Bladder Cells	500; 6w	>12w
MN	<i>M. crystallinum</i>	Side Shoots	500; 3 d	6w
MO	<i>M. crystallinum</i>	Meristems	No Stress	5w
MP	<i>M. crystallinum</i>	Meristems	500; 3 d	6w
NA	<i>N. tabacum</i> (SR1)	Roots & Leaves	200; 6,24,30,48h	4w
NB	<i>N. tabacum</i> (SR1)	Leaves	No Stress	~10w
OA	<i>O. sativa</i> (Nipponbare)	Root	200; 19h	3-4w
OB	<i>O. sativa</i> (Nipponbare)	Leaves	200; 19h	3-4w
OC	<i>O. sativa</i> (Pokkali)	Roots	No Stress	1w
OD	<i>O. sativa</i> (Pokkali)	Roots	150; 1d	1w
OE	<i>O. sativa</i> (Pokkali)	Roots	150; 2;3d	1w
OF	<i>O. sativa</i> (Pokkali)	Roots	150; 1w	2w
OG	<i>O. sativa</i> (Pokkali)	Leaves	150; 1; 2; 3d; 1w	1w
OH	<i>O. sativa</i> (Pokkali)	Leaves	No Stress	1-2w
ZA	<i>Z. mays</i> (B73)	Roots	150; 24h	2w
ZB	<i>Z. mays</i> (B73)	Leaves & Shoots	150; 24h	2w

Table II: Abundance profile of ESTs in a root cDNA library of salt-stressed corn.

Gene Category	No. of ESTs	% of Total	Category Description
No hit	493	26.2	Blast search in non-redundant GenBank finds no homologs
Unknown	296	15.7	Blast search GenBank identifies unknown, hypothetical, and putative protein, or proteins with unknown functions
Metabolism	203	10.8	Amino -acid, nucleotide, C-compound and carbohydrate, lipid, fatty-acid and isoprenoid, nitrogen and sulfur, and secondary metabolisms
Cell rescue, defense	165	8.8	Environmental stimuli responses (stress, wounding, phytohormone regulation, and ions deficiency), radical scavenging, detoxification, DNA repair, and cell death
Protein synthesis	123	6.5	Ribosomal proteins, translation (initiation, elongation and termination), translational control, and tRNA synthetases
Energy	111	5.9	Glycolysis and gluconeogenesis, pentose-phosphate pathway, TCA pathway, respiration, metabolism of energy reserves (e.g., glycogen, trehalose), and fatty acid oxidation
Transport facilitation	76	4.0	Ion channels, water channels, ion, sugar and carbohydrate, amino acid, lipid, purine and pyrimidine transporters, transport ATPases
Protein destination	76	4.0	Protein folding and stabilization, protein targeting, sorting and translocation, protein modification (e.g., myristylation, farnesylation, palmitoylation, glycosylation) and proteolysis
Signal transduction	75	4.0	Receptor proteins, second messenger such as calmodulins, key kinases, key phosphatases, and G-proteins
Cell growth, division	74	3.9	Cell growth, development, cell cycle control and mitosis, cytokinesis, and DNA synthesis and replication
Transcription	71	3.8	mRNA synthesis (including general transcription activities, transcriptional control such as transcriptional factors, and chromatin modification), mRNA splicing, and mRNA stabilization and degradation
Photo-synthesis	63	3.3	Chlorophyll a/b-binding protein, Ferredoxin related genes, photosystem I & II reaction center
Metal ion homeostasis	39	2.1	Homeostasis of metal ions and other ions
Intracellular Transport	17	0.9	Vesicular transport (Golgi network), vacuolar transport, cytoskeleton-dependent transport
Total	1,882	100	

Table III: Abundance profile of ESTs in a leaf cDNA library of salt-stressed rice cv. Pokkali (OG).

Gene Category	No. of ESTs	% of Total	Category Description
No hit	16	3.4	Blast search in non-redundant GenBank finds no homologs
Unknown	97	20.8	Blast search GenBank identifies unknown, hypothetical, and putative protein, or proteins with unknown functions
Metabolism	37	7.9	Amino -acid, nucleotide, C-compound and carbohydrate, lipid, fatty-acid and isoprenoid, nitrogen and sulfur, and secondary metabolisms
Cell rescue, defense	29	6.2	Environmental stimuli responses (stress, wounding, phytohormone regulation, and ions deficiency), radical scavenging, detoxification, DNA repair, and cell death
Protein synthesis	27	5.8	Ribosomal proteins, translation (initiation, elongation and termination), translational control, and tRNA synthetases
Energy	13	2.8	Glycolysis and gluconeogenesis, pentose-phosphate pathway, TCA pathway, respiration, metabolism of energy reserves (e.g.glycogen, trehalose), and fatty acid oxidation
Transport facilitation	11	2.4	Ion channels, water channels, ion, sugar and carbohydrate, amino acid, lipid, purine and pyrimidine transporters, transport ATPases
Protein destination	91	20.4	Protein folding and stabilization, protein targeting, sorting and translocation, protein modification (myristylation, farnesylation, palmitoylation, glycosylation) and proteolysis
Signal transduction	21	4.5	Receptor proteins, second messenger such as calmodulins, key kinases, key phosphatases, and G-proteins
Cell growth, division	10	2.1	Cell growth, development, cell cycle control and mitosis, cytokinesis, and DNA synthesis, replication, and repair
Transcription	13	2.8	mRNA synthesis (including general transcription activities, transcriptional control such as transcriptional factors, and chromatin modification), mRNA splicing, and mRNA stabilization and degradation
Photoynthesis	156	33.5	Chlorophyll a/b-binding protein, Ferredoxin related genes, photosystem I & II reaction center
Metal ion homeostasis	0	0	Homeostasis of metal ions and other ions
Cell structure	16	3.4	Cytoskeletal and other structural proteins (e.g., actin, histones)
Transposons	5	1.1	Transposition-related activities (En/Spm-like proteins)
Total	446	100	

Table IV: Stress Model Organism EST PipeOnline_v2.0b database descriptions^a

^aBased on the assumption that libraries are mRNA populations representative and tags selected through random sampling. ^bPOL_db and the PipeOnline_v2.0b automated DNA sequence processing and functional sorting package are described (stress-genomics.org) [Ayoubi P., Jin X., Leite S., Liu X., Martajaja J., Abduraham R., Wan Q., Yan W., Misawa E., Prade R.A., unpublished]. Full and unrestricted database access for all the models listed are available from the stress-genomics.org website. ^cESTs downloaded from dEST

Surveyed EST libraries	ESTs		POLdb record with HSP >100 ^b					
	all	unique	Total		Function		no Function	
			#	%	#	%	#	%
PLANT MODELS								
<i>Arabidopsis thaliana</i>	3,336	2,379	1,495	63	371	25	1,124	75
<i>Hordeum vulgare</i>	576	537	308	57	95	31	213	69
<i>M. crystallinum</i>	7,327	3,788	2,096	55	567	27	1,529	73
<i>Oryza sativa</i>	3,816	2,553	1,224	48	322	26	902	74
<i>Dunaliella salina</i>	2,052	1,243	622	50	201	32	421	68
<i>Selaginella</i> sp.	1,191	995	769	77	215	28	554	72
All plant models	18,298	11,495	6,514		1,771		4,743	
Plant Model Average	3,050	1,916	1,086	58	295	28	791	72
GENOMIC MODEL SYSTEMS								
<i>Aspergillus nidulans</i> ^c	12,485	4,595	1,863	41	609	33	1,254	67
<i>S. cerevisiae</i> ^c	2,799	1,587	1,343	85	318	24	1,025	76
All genomic models	15,284	6,182	3,206		927		2,279	
Genomic Model Average	7,642	3,091		63		28		72
All biological systems	30,783	16,090	8,377		2,380		5,997	
Overall Average	3,848	2,011		61		28		72

Table V: Selected ESTs highly expressed in either EBC or shoots in *Mesembryanthemum.**

*Data from microarray slides containing ~2,600 EST elements. Ratio shoot/EBC and EBC/shoot for a selected number of transcripts from two independent hybridization experiments are shown. EBC - epidermal bladder cells.

Expt 1	Expt 2	Clone ID#	Annotation	Homology	Functional categories
EBC-specific ESTs					
12.8	34.4	MH03A05	anti-fungal protein 1 precursor	P81418 pokeweed	Cell Rescue, Defense, Cell Death, and Ageing
9.4	12.3	ML02G10	annotation in progress	-	NA
6.9	8.8	MO01F11	carboxyphosphoenolpyruvate mutase	S35145 carnation	Metabolism
9.7	8.5	MG04B05	major allergen Mal d1, pathogenesis related	S11869 potato	Cell Rescue, Defense, Cell Death, and Ageing
29.3	8.1	MH02C01	antimicrobial peptide, AMP2	P81418 pokeweed	Cell Rescue, Defense, Cell Death, and Ageing
2.5	7.4	MH01C03	pathogenesis-related protein 5 precursor, thaumatin	P28493 <i>Arabidopsis</i>	Cell Rescue, Defense, Cell Death, and Ageing
9.3	6.9	MM04F08	major allergen Mal d1, pathogenesis related	Z72425 apple tree	Cell Rescue, Defense, Cell Death, and Ageing
3.8	6.5	MH02C02	receptor-like protein kinase	AC000132 <i>Arabidopsis</i>	Signal Transduction
4.9	5.3	MF07F05	no hits	-	NA
2.1	4.8	MP09D06	no hits	-	NA
4.0	4.8	ML01E05	no hits	-	NA
4.9	4.6	ML03C02	nonspecific lipid-transfer protein	Q43748 sugarbeet	Cellular Organization
8.8	4.6	MK01E03	no hits	-	NA
6.9	4.1	MM01G02	unknown	AB003280 <i>Arabidopsis</i>	NA
8.6	3.5	MM02F06	annotation in progress	-	NA
Shoot-specific cDNAs					
24.6	3.9	MP03C10	unknown, desiccation-related protein 2	P22242 <i>C.plantagineum</i>	Cell Rescue, Defense, Cell Death, and Ageing
15.2	3.8	MH02D01	BURP-domain containing protein	AC007504 <i>Arabidopsis</i>	NA
16.4	3.9	MO03G01	vegetative storage protein, wound induced	S39502 poplar	NA
9.8	3.8	MO02E11	lipid transfer protein, glossy (gl1) homolog	L33792 <i>S.odoros</i>	Cellular Organization
8.9	3.8	MP07B01	water channel, tonoplast membrane, MIP-F	U43291 ice plant	Transport Facilitation
7.3	3.8	MG01A01	no hits	-	NA
6.9	3.8	ME02E06	unknown, jasmonate-induced protein	P42764 <i>Atriplex</i>	NA
6.3	3.7	MG04B01	no hits	-	NA
5.7	3.7	MG01A07	unknown	AF024504 <i>Arabidopsis</i>	NA
5.2	3.7	MP14F03	water channel, plasma membrane, MIP A	L36095 ice plant	Transport Facilitation
4.9	3.6	R30-tip#2	water channel, tonoplast membrane, MIP I	AF133531 ice plant	Transport Facilitation
4.9	3.6	R30-tip#18	lipoygenase	AF145479 ice plant	Metabolism/ Signal transduction
4.8	3.6	MP14B04	chitinase	JC4053 pokeweed	Cell Rescue, Defense, Death, and Aging
4.8	3.6	MP01G05	cysteine proteinase	U30322 ice plant	Protein Destination
4.8	3.6	MP14C02	unknown	P13729 fruit fly	NA

Table VI: Frequencies of mutants isolated as variants in responsiveness of the RD29A promoter or as salt tolerant or sensitive. All indicated mutants have been confirmed by a second screen of progeny from self-fertilized T₂ mutants

	Phenotype of mutant	Population screened
1.	<u>hos/los</u> 43 hos 20 los	80,000
2.	<u>sos3 suppressors</u> 5 <i>sos3</i> suppressors 13 suppressors of part of the <i>sos3</i> syndrome	55,000
3.	Salt tolerant 3	10,000
4.	Salt sensitive 12	50,000

Table VII. Screens of 35,000 (T₂) T-DNA insertion mutant lines of C24 ecotype.

All mutants were generated by transformation with the pSKI vector described by Weigel *et al.* [48] and confirmed in progeny of T₂ plants except as indicated. Many possible visible phenotypes were not carefully examined. For example, populations were not inspected for floral structure variants. Agamous-like variants were observed as continuous flowering.

Phenotype	No. found in T2 Pop.
dwarf	11
eceriferum	7
glabrous	9
elongated spatulate leaves	3
thin strap-like leaves and petals	2
wrinkled/cupped leaves	7
cauliflower inflorescence	1
agamous-like	2
late flower	9
pin-like	2
dark green leaves	5
light green leaves	3
small leaves	4
round leaves	2
multi-branch shoot	5
curled leaf	2
upright siliques	1
reduced fecundity	20
miscellaneous unverified/steriles	33
putative mutants that were wildtype in T3	58

Table VIII: Plant ESTs homologous to salt stress-induced yeast ORFs*.

*Yeast ORFs upregulated during salt stress (1M, 10, 30 and 90 min) are described [50].

**For MIPS classification see <http://websvr.mips.biochem.mpg.de/proj/yeast/catalogues/funcat/>.

Systematic name	Gene name	Functional annotation	**MIPS category	Mesemb.	Rice	Corn
YPL218W	SAR1	GTP-binding protein of the ARF family	INTTRA	ME01G01		
YJR009C	TDH2	glyceraldehyde-3-phosphate dehydrogenase 2	MET	ME02A12	OD105G05	
YAL004W*		strong similarity to <i>A.klebsiana</i> glutamate dehydrogenase	U	ME02D10		
YAL005C*	SSA1	heat shock protein of HSP70 family, cytosolic	CDEF	ME02D10	OC11H04	
YKR014C	YPT52	GTP-binding protein of the rab family	PDEST	ME02H03	OC104H06	
YBL087C	RPL23A	60S large subunit ribosomal protein L23.e	PS	ME03G02	OC10A11	ZA5740407
YER103W	SSA4	heat shock protein of HSP70 family, cytosolic	CDEF	ME04D06		
YGL166W*	CUP2	copper-dependent transcription factor	TRANSC	MF02C06		
YJL190C	RPS24A	ribosomal protein S15a.e.c10	PS	MF02C10	OC01A08	
YHR049C-A*		questionable ORF	U	MF02E11		
YPL079W	RPL21B	ribosomal protein L21	PS	MF03B08		
YEL059W		hypothetical protein	U	MF04B05		
YIL052C	RPL34B	ribosomal protein L34.e	PS	MF05B01		
YNL192W	CHS1	chitin synthase I	MET	MF06B02		
YER130C		similarity to MSN2P and weak similarity to MSN4P	U	MF07E01		
YGR137W		questionable ORF	U	MF07G10		
YMR110C		similarity to aldehyde dehydrogenase	U	MG01A11		
YDR055W	PST1	strong similarity to SPS2 protein	U	MG01D06		
YLR167W	UBI3	ubiquitin/40S small subunit ribosomal protein	PS	MG01D09	OE11C03	ZA0C265
YER141W	COX15	cytochrome oxidase assembly factor	MET	MG01E08		
YPR035W	GLN1	glutamate--ammonia ligase	MET	MG01E12		
YJR121W	ATP2	F1F0-ATPase complex, F1 beta subunit	IONHOM	MG02C10	OC03G05	
YDR064W	RPS13C	ribosomal protein	PS	MG04E09		
YDR461W	MFA1	mating pheromone a-factor 1	CGRO	MG05D01		
YGL165C*		questionable ORF	U	MG05D03	OF03D10	
YHR137W*	ARO9	aromatic amino acid aminotransferase II	MET	MG05F04		
YMR186W	HSC82	heat shock protein	CDEF	MH01B05	OC09E02	
YLR029C	RPL15A	RPL15A 60s large subunit ribosomal protein L15.e.c12	PS	MH01G05		
YKL036C*		questionable ORF	U	MH03B02		
YLR333C	RPS31	ribosomal protein S25.e.c12	PS	MH04B07		
YPL090C	RPS6A	ribosomal protein S6.e	PS	MH05B07	OE08E07	
YOL087C		similarity to <i>S.pombe</i> hypothetical protein	U	MH05E12		
YLR293C	GSP1	GTP-binding protein of the ras superfamily	TRANSC	MH05H04		ZA4730320
YAL003W	EFB1	translation elongation factor eEF1beta	TL		OC01C02	
YGL248W	PDE1	low affinity 3',5'-cyclic-nucleotide phosphodiesterase	MET		OC02B01	
YGR085C	RPL11B	ribosomal protein	PS		OC08H01	
YLL026W	HSP104	heat shock protein	CDEF		OC101B09	
YML001W	YPT7	GTP-binding protein of the RAB family	INTTRA		OC104H06	
YPL081W	RPS9A	ribosomal protein S9.e.A	PS		OC105A09	ZA5740676
YEL054C	RPL15B	60S large subunit ribosomal protein L12.e	PS		OC105B04	

YGL147C	RPL9A	ribosomal protein L9.e	PS	OC10B09	ZA5739836
YKL100C		similarity to C.elegans hypothetical protein	U	OD103H07	
YHR203C	RPS7A	RPS4B ribosomal protein S4.e.c8	PS	OE03C03	
YDR154C*		questionable ORF	U	OE05B12	
YDR155C*	CPH1	cyclophilin (peptidylprolyl isomerase)	PDEST	OE05B12	
YDR025W	RPS18A	ribosomal protein S11.e	PS	OE07F09	
YDR304C	CYP5	peptidyl-prolyl cis-trans isomerase D precursor(cyclophilin D) of the ER	MET	OE10D02	
YOL040C	RPS21	RPS15, 40S small subunit ribosomal protein	PS	OE14G07	
YMR119W-A		questionable ORF	U	OE202E11	
YER067W		strong similarity to hypothetical protein YIL057c	U	OF03D09	
YJL053W	PEP8	vacuolar protein sorting/targeting protein	PDEST		ZA0C131
YJL138C	TIF2	translation initiation factor eIF4A	PS		ZA0C157
YEL024W	RIP1	ubiquinol--cytochrome-c reductase iron-sulfur protein precursor	ENERGY		ZA0C93
YBL027W	RPL19A	60S large subunit ribosomal protein L19.e	PS		ZA5739792
YGR086C		strong similarity to hypothetical protein YPL004c	U		ZA5757355

Table IX: Selected *Synechocystis* PCC6803 genes with homology to yeast stress-induced ORFs and higher plant stress-related ESTs. Table representing a selected list of Blast hits from higher plant Salt Stressed EST sequences against the *Synechocystis* PCC6803 (whole genomic) amino acid sequence. Of the 11,194 salt stress EST's queried, 1,964 show homology to *Synechocystis*. Tissue types are as follows: R-Roots, L-Leaves, F&S-Flowers and Seedpods, S-Seedlings, BC-Bladder Cells, WS-Whole Seedlings, M-Meristems.

Functional Category	<i>Synechocystis</i> Gene	Yeast	Rice	Barley	Ice Plant	Arabidopsis
Light Regulated	CAB/ELIP/HLIP superfamily	-	-	-	R/L	L
	highlight-inducible protein	-	-	-	"M, F&S"	L
Chaperonins	DnaJ protein	-	R	"L, R"	"M, WS"	L
	plastocyanin	-	-	-	"M, F&S"	"L, R, WS"
	10kD chaperonin	-	-	-	"M, BC"	L
	DnaK protein	Y	R	R	All	"L, R"
	60kD chaperonin	-	-	-	M	All
Oxidative Stress	catalase hpi(katG)	Y	-	R	"R, F&S,M"	"L, R"
	thiol-specific antioxidant protein	-	R	-	M	"L, R"
	glutaredoxin 3	Y	R	-	"R, M"	L
	glutathione peroxidase	Y	-	L	2' L	"L, R"
	membrane protein	-	R	-	R	L
	superoxide dismutase	Y	-	-	M	L
	Ycf39	-	-	-	R	"L, R, WS"
Transporters	Na ⁺ /H ⁺ -antiporter	Y	-	-	-	-
	Na-ATPase(PacL)	Y	-	-	-	-
	ABCtransporter	-	R	-	"R, M, F&S"	-
	water channel	-	R	R	"R, M, S"	All
	spore protein sp21	-	-	R	"R, M"	-
	salt-stress hydrophobic peptide	-	R	-	"R, M, BC"	"L, R, WS"
	high affinity sulfate transporter	Y	-	-	-	WS
	cation-transporting ATPase PacL	-	-	-	BC	L
Translational Factors	initiationfactor IF-2	-	R	R	"R, M, F&S"	"L, R"
	RNA-binding protein	-	R	L	"R, M, F&S, BC"	all
	elongationfactor Tu	-	R	"L, R"	"R, M, F&S"	L
Kinases and Phosphatases	monophosphatase	Y	-	-	-	-
	extragenic suppressor SuhB	Y	R	-	-	"L, R"
	protein kinase PknA	Y	-	-	R	R
	protein kinase C inhibitor	-	R	-	R	-
	serine esterase	Y	-	-	R	-
	eukaryotic protein kinase	Y	R	R	"R, M, F&S"	L
	sensory transduction histidine kinase	-	R	-	-	"L, R"
	betatransducin-like protein	-	R	-	"R, M"	"L, R, WS"
Carbon Concentration Energy Metabolism	ferredoxin-NADP oxidoreductase	Y	R	-	-	"L, WS"
	UDP-glucose dehydrogenase	-	R	"L, R"	-	"L, R"
	S-adenosylhomocysteine hydrolase	-	R	R	"R, M, F&S"	"L, R"
Hypothetical	Hypothetical proteins	Y	many	many	many	many