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Rapid Communication

Identification of *Arabidopsis* Genes Regulated by High Light–Stress Using cDNA Microarray¶

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ABSTRACT

In plants, excess light has the potential to damage the photosynthetic apparatus. The damage is caused in part by reactive oxygen species (ROS) generated by electrons leaking from the photosynthetic electron transport system. To investigate the mechanisms equipped in higher plants to reduce high light (HL) stress, we surveyed the response of 7000 *Arabidopsis* genes to HL, taking advantage of the recently developed microarray technology. Our analysis revealed that 110 genes had a positive response to a 3 h treatment at a light intensity of 150 W m^{-2}. In addition to the scavenging enzymes of ROS, the genes involved in biosynthesis of lignins and flavonoids are activated by HL and actually resulted in increased accumulation of lignins and anthocyanins. Comparing the HL-responsive genes with drought-inducible genes identified with the same microarray system revealed a dense overlap between HL- and drought-inducible genes. In addition, we have identified 10 genes that showed upregulation by HL, drought, cold and also salt stress. These genes include *RD29A, ERD7, ERD10, KIN1, LEA14* and *COR15a,* most of which are thought to be involved in the protection of cellular components.

INTRODUCTION

For plants, photosynthesis is the one and only source of energy, and thus limited light causes limited growth. However, exposure to excess light relative to the photosynthetic capacity has the potential to damage cells, in part by reactive oxygen species (ROS) generated by excitation energy and electrons leaking from the photochemical reactions and electron transport system. However, plants have developed several strategies to protect their cells. These include the development of ROS scavengers such as peroxidases, accumulation of anthocyanins to reduce light intensity within tissues, reduction of antenna components and also the development of systems to dissipate absorbed light energy (1,2). Some of the responses are known to be regulated at the level of gene expression.

Using *Arabidopsis* as a model plant, previous studies have identified several genes that are activated by high intensity light (HL). These include genes for chalcone synthase (3), ROS scavengers (4), stress-related members of the *CAB* superfamily (5) and a putative transcription factor (6). Recently, RNA differential display experiments were carried out that identified some more HL-inducible genes (7). In contrast, antenna components (LHCP) have been shown to be down-regulated by HL (5).

The recent development of microarray technology for monitoring the expression of thousands of genes at a time has enabled comprehensive analysis of the responses of gene expression to HL, as demonstrated in a cyanobacterial study (8). Taking advantage of this powerful method, we decided to investigate responses to HL stress in *Arabidopsis*. Using a RIKEN cDNA (cDNA) microarray system representing 7000 independent genes (9), 110 genes have been revealed to show activation by HL. Parallel experiments for drought responses using the same microarray system (9) showed that about 70% of the HL-induced genes were also induced by drought stress, revealing a dense overlap between HL and drought responses.

MATERIALS AND METHODS

Microarray analysis. Seeds of *Arabidopsis thaliana* Col were germinated and grown on Germination Medium (GM) containing 1% sucrose and 0.8% Bactoagar (Difco, Detroit, MI) at 22°C under continuous white light (6 W m^{-2}). Ten day old seedlings were treated with HL (150 W m^{-2}) generated by a xenon lamp for 3 h as reported previously (10). The aerial part of the

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Abbreviations: ETS, the photosynthetic electron transport system; GM, Germination Medium; HL, high light; LL, low light; mRNA, messenger RNA; ROS, reactive oxygen species.
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Table 1. The primers and PCR cycle conditions for quantitative RT-PCR analysis

Gene	Primers		Cycle*	Anneal (°C)†
RAFL09-10-I03	gtt gga tga gat cag aaa gg	gct tcg tct aga ctc tta ac	19, 21, 23	53
RAFL09-06-O18	ctc cgt gaa ctc atc agt aa	tag aga aag cct cgt aga ac	15, 17, 19	53
RAFL05-04-J06	ccg aac cca aat ctc ttt ac	tta agc agt aac tcc caa ca	19, 21, 23	53
RAFL04-09-J20	tag aat cgc gat tcc gat aa	cac cca aag atc tta agc ag	17, 19, 21	53
RAFL04-12-M20	tat tga cta cac gca aca tca gaa	gtt ttc tcc ctt tga taa ctc cat	19, 21, 23	53

*Cycle number used for quantification of PCR products.
†Annealing temperature of the reaction. For other experimental conditions, see Kimura *et al.* (10).

seedlings from four independent experiments was harvested and pooled, and total RNA was extracted as described in Yamamoto *et al.* (11). PolyA$^+$ RNA samples were purified using the Oligotex™-dT$_{30}$ messenger RNA (mRNA) purification kit (Roche Diagnostics, Tokyo, Japan) according to the manufacturer's instructions. PolyA$^+$ RNA samples were then labeled, hybridized with the RIKEN cDNA microarray covering 7000 full-length cDNA fragments (9), washed and scanned, and each signal was quantified exactly as described previously (12). Labeling and hybridization was achieved independently for three times, and the response was expressed as an average of the ratio of HL-treated sample to untreated sample. Quantified hybridization data were analyzed using Excel software (Microsoft Japan, Tokyo, Japan) together with homemade Perl tools. Sequences of RIKEN *Arabidopsis* Full-Length (RAFL) cDNA clones (13) have been determined by the *Arabidopsis* Salk/Stanford/PGEC (SSP)-sequencing consortium (http://signal.salk.edu/SSP/index.html), and the sequence information can be found at DNA Databank of Japan (DDBJ) and Genbank databases. Further information can be found at our website (http://www.gsc.riken.go.jp/Plant/). Some of the RAFL cDNA clones are available from RIKEN Bioresource Center (http://www.brc.riken.go.jp/Eng/e-plant.html). *Arabidopsis* photosynthesis-related genes were primarily identified following Legen *et al.* (14). Further information about the *Arabidopsis* genes was obtained from the following databases on the web: http://www.arabidopsis.org/, http://www.tigr.org/tdb/e2k1/ath1/, http://mips.gsf.de/proj/thal/db/ and http://www.ncbi.nlm.nih.gov/.The supplemental data from this study (tables) are available at http://www.gsc.riken.go.jp/Plant/index.html.

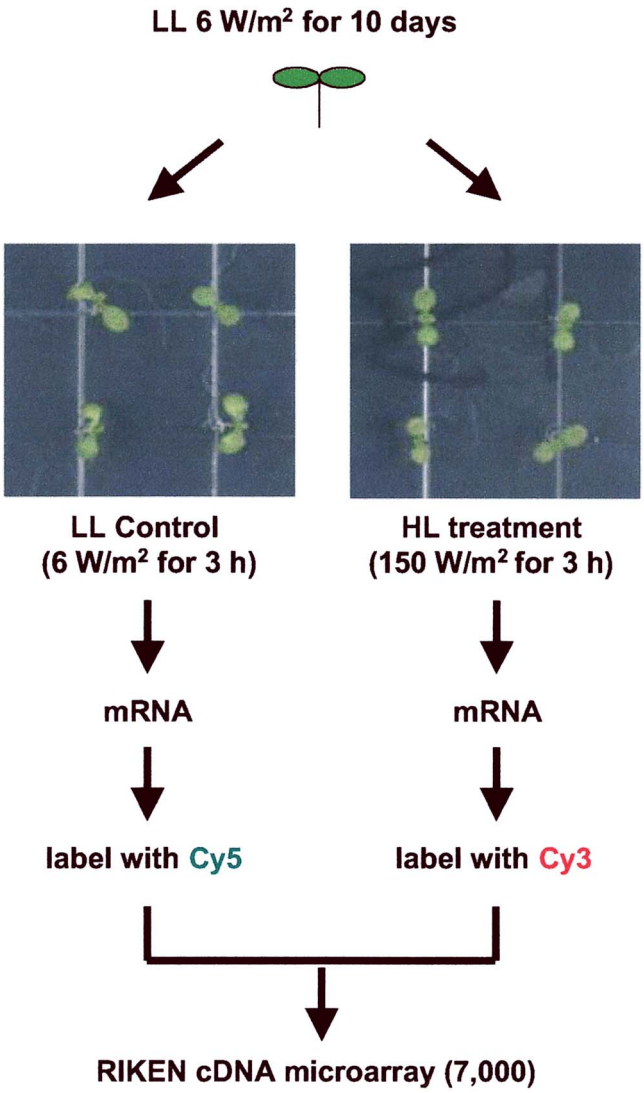

Figure 1. Experimental scheme of the microarray analysis. Photograph is a representation of seedlings after treatment. Seedlings were grown more densely for the analysis than shown in the pictures.

Lignin and anthocyanin quantification. Seedlings grown under low-light (LL) conditions were treated with HL (10), and the aerial parts of the seedlings were harvested and frozen in liquid nitrogen, and the lignin content was analyzed by the triglycoic acid (TGA) method (15). Anthocyanin amounts were quantified as described in a previous report (16). Long-term treatments with HL (90 W m^{-2}) were achieved by illumination with fluorescent tubes (FPR96EX-NA, National, Kadoma, Japan) in a growth chamber at 22°C.

Quantitative reverse transcriptase–polymerase chain reaction. The aerial parts of 10 day old seedlings were treated with HL at the indicated intensities and harvested, and total RNA was extracted. Quantitative reverse transcriptase–polymerase chain reaction (RT-PCR) analysis was performed essentially as described previously (10). Primer sequence, annealing temperature and cycle number used for quantification were altered depending on gene copy number as shown in Table 1.

RESULTS AND DISCUSSION

Arabidopsis seedlings grown under continuous LL (6 W m^{-2}, equivalent to *ca* 30 μE m^{-2} s^{-1}) were treated with HL of 150 W m^{-2} (*ca* 800 μE m^{-2} s^{-1}) for 3 h. Material was harvested together with that from control seedlings and subjected to microarray analysis as summarized in Fig. 1. To avoid the effects of UV light and heat, filters were used to remove UV light and infrared components from the HL source, leaving only visible light (400–700 nm; for the spectrum, see Kimura *et al.* [10]). During the HL treatments, the change in temperature of the medium was less than 1°C. HL treatments were carried out so as to avoid drought stress as well (10), as shown in Fig. 1. The sampling time of the treated seedlings was the same as that of the control, so that the effects of circadian rhythm were negligible. Among the 7000 clones, 3232 clones showed detectable signals that were more than two-fold stronger than those of the negative controls for both HL-treated and control probes.

Genes up-regulated by HL

Among the 3000 expressed genes, 110 genes were revealed to be up-regulated by the HL treatment more than three-fold. The list of

Table 2. The HL-inducible genes reported in previous work*

Clone name	Gene	Ratio	SD	MIPS
RAFL04-12-M20	*ELIP2* (5,10)	22.53	10.80	At4g14690
RAFL11-09-C12	Metallothionein-like protein (7)	9.34	3.41	At1g07600
RAFL09-06-P19	Putative fibrillin (17)	7.67	2.19	At4g04020
RAFL05-12-M18	Putative ascorbate peroxidase (4)	5.04	0.54	At4g09010
RAFL09-16-P08	Glutathione reductase (4)	3.60	0.84	At3g24170
RAFL09-10-I03	Chalcone synthase (3)	3.53	0.51	At5g13930

*HL response is calculated as a ratio of hybridization signal of the HL-treated sample to the control from an average of three experiments (ratio), and the corresponding standard deviations (SD) are shown together with the MIPS protein code (MIPS).

clones is shown in Table S1, which is also available at http://www.gsc.riken.go.jp/Plant/index.html and the journal website [www.aspjournal.com]. Among them, two genes, *ELIP2* (At4g14690) and a metallothionein-like gene (At1g07600), have been studied previously for their HL responses (5,7,10). The induction of some other genes has been suggested on the basis of HL response of the homologs in *Arabidopsis* or other plant species (fibrillin, ascorbate peroxidase, glutathione reductase and chalcone synthase [3,4,17]). These examples, which are consistent with the findings of previous reports, are listed in Table 2.

ROS scavengers

HL treatment is known to cause the evolution of ROS within the chloroplast, and several ROS scavengers have been shown to be induced by HL (4). Figure 2 summarizes the functions of scavengers and their response to HL. The figure represents only genes identified from the spotted clones of the microarray, and hypothetical genes with sequence homology to the enzymes are shown with an "h" suffix after the enzyme name. As shown in the figure, GR and PHGPX were upregulated by HL, and SOD, MDAR and GSH-DHAR did not respond. Among the GST and peroxidase families, some gene copies were activated, whereas the other copies were not, demonstrating differential responses within gene families.

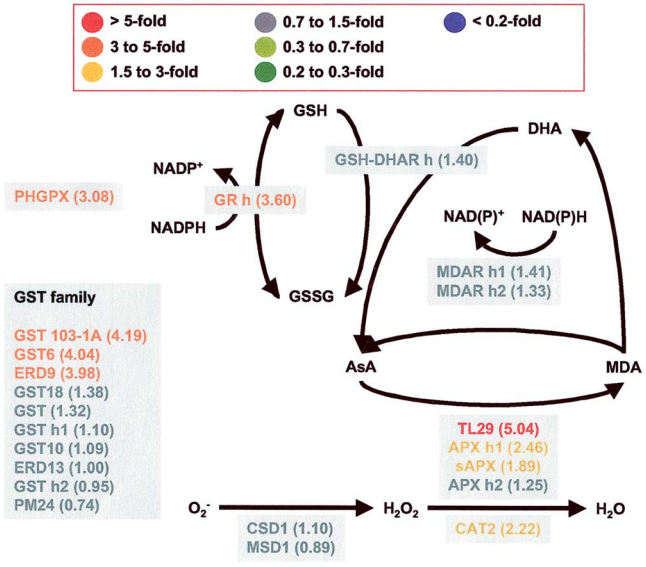

Figure 2. Response of detoxification enzymes to HL. HL response is classified according to magnitude, and each class is represented in the same color as shown in the top panel. Clone name and standard deviation of the response are shown in Table S2. APX, ascorbate peroxidase; AsA, ascorbate; CAT, catalase; DHA, dehydroascorbate; GR, glutathione reductase; GSH-DHAR, GSH-dependent dehydroascorbate reductase; GST, glutathione *S*-transferase; MDA, monodehydroascorbate; MDAR, monodehydroascorbate reductase; PHGPX, phospholipid hydroperoxide-dependent glutathione peroxidase. TL29 is a putative ascorbate peroxidase.

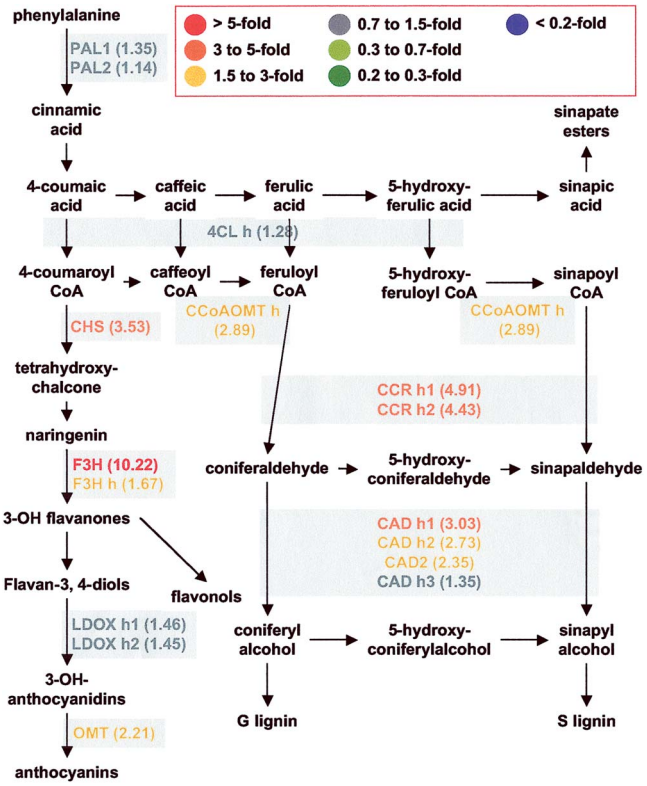

Figure 3. Response of genes in the phenylpropanoid pathway to HL. Clone name and standard deviation of the response are shown in Table S3. CAD, cinnamyl-alcohol dehydrogenase; CCR, cinnamoyl-CoA reductase; CCoAOM, caffeoyl-CoA *O*-methyltransferase; CHS, chalcone synthase; LDOX, leucoanthocyanidin dioxygenase; OMT, *O*-methyltransferase; PAL, phenylalanine ammonia lyase. For more detail, see Fig. 2.

Enzymes for the phenylpropanoid pathways

Although HL is known to activate expression of the chalcone synthase gene (3), it is not known whether other flavonoid biosynthesis genes respond to the stress. Figure 3 shows the flavonoid biosynthesis pathway together with the responses in expression. Among the enzymes shown in the figure, most of the genes after 4-coumarate-CoA ligase were activated by HL treatment, especially F3H, which showed high induction by the treatment. These expression profiles predict that not only anthocyanin but also lignin biosynthesis is activated by HL.

To examine whether such activation at the mRNA level is reflected in flavonoid biosynthesis, the effect of HL on the accumulation of anthocyanin and lignin was examined. Figure 4A shows that HL treatment stimulates anthocyanin accumulation, which is consistent with previous reports (18). Figure 4B shows the

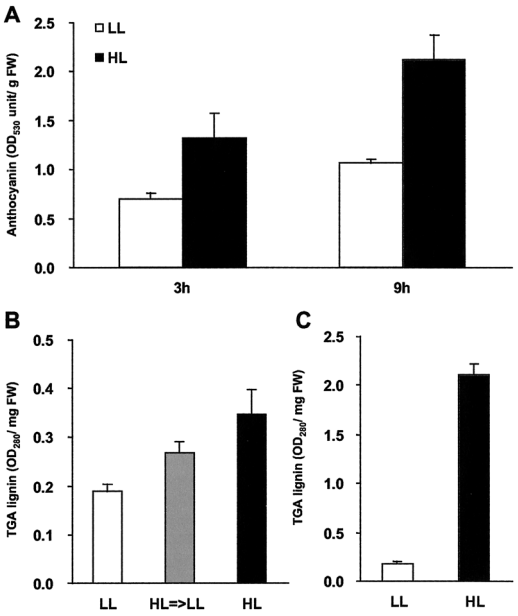

Figure 4. Anthocyanin and lignin accumulation affected by HL stress. A: Anthocyanin accumulation by HL treatments. Ten day old seedlings grown under LL conditions (6 W m^{-2}) were treated with HL (150 W m^{-2}) or LL (6 W m^{-2}) for the period indicated. Average and standard deviation of the anthocyanin amount on the basis of fresh weight (FW) are shown. B: Lignin accumulation by HL treatments. Ten day old seedlings grown under LL conditions (6 W m^{-2}) were treated with HL (150 W m^{-2}) for 3 h followed by LL for 9 h (HL → LL) or 12 h (HL). Average and standard deviation are shown. C: Slow response of lignin accumulation by HL treatment. Two week old seedlings grown under LL conditions (6 W m^{-2}) were treated with moderate HL (90 W m^{-2}) and grown for 1 week. Average and standard deviation of the lignin amount on the basis of FW are shown.

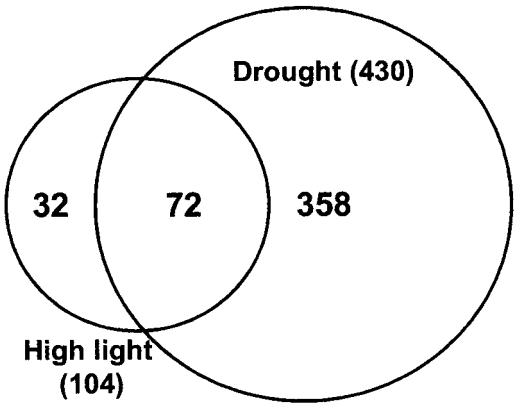

Figure 5. HL- and drought-inducible genes. Relationship between drought- and HL-responsive genes is shown. Drought-responsive genes have been identified in a previous study (9), and a three-fold induction by 2 or 5 h treatments was used as the threshold for a positive response. Numbers of genes are indicated.

change in lignin accumulation in response to HL. A 3 h treatment with HL followed by 9 h of incubation under LL resulted in a detectable increase in lignin content (LL *vs* HL → LL). Continuous treatment with HL for 12 h resulted in a clearer response (HL). Figure 4C shows a slower response to HL, and in this experiment, seedlings grown under LL (6 W m^{-2}, equivalent to *ca* 30 μE m^{-2} s^{-1}) were treated with moderate HL (90 W m^{-2}, equivalent to *ca* 400 μE m^{-2} s^{-1}) for a week, whereas the control plants were left under LL for the same period. As shown in the figure, lignin accumulation increased strikingly during the long incubation period. These results indicate that activation of gene expression by HL led to increases of anthocyanin and lignin accumulation. This is the first report to show HL stimulation of lignin accumulation in higher plants.

Signal transducers and transcriptional factors show upregulation by light stress

Table 3 shows (possible) signal transducers that showed HL activation. Their inductive nature suggests that they are involved in HL signal transduction (19). Interestingly, Sig5 (also called SigE), a transcriptional regulator of a subset of the chloroplast-encoded genes (20), was found to respond to light stress. This may suggest differential regulation of plastidic gene expression by light stress through *Sig5*.

Cross talk between drought and other stress responses

Among the HL-inducible genes shown in Table S1, some are also known to be induced by other stresses such as drought, cold or heat. These include *RAB, RD, ERD, COR, KIN, LEA, AtGolS, HSP,* lipid-transfer proteins and fibrillins (9,21). Fibrillin is a component of plastoglobules, which are plastidic globular structures containing lipids, proteins and carotenoids (21). The fact

Table 3. HL-inducible signal transducers and transcription factors*

Clone name	Gene	Ratio	SD
RAFL08-16-M12	RD20 (putative Ca^{2+}-binding EF-hand protein)	10.42	3.54
RAFL11-11-C18	Protein serine/threonine kinase-like protein	7.73	3.90
RAFL06-08-H20	AP2 domain-containing protein	5.91	1.30
RAFL07-07-G15	NAC domain protein	5.22	0.52
RAFL05-16-H23	Putative DNA-binding protein AP2 domain-containing protein *RAP2.4*	5.08	1.37
RAFL04-09-J20	NaCl-inducible Ca^{2+}-binding protein-like	4.74	0.61
RAFL08-08-L21	*Sig*5	4.41	1.34
RAFL11-01-J18	Homeobox-leucine zipper protein *ATHB-12*	3.10	0.62
RAFL06-12-A20	Putative RING-H2 zinc finger protein	3.53	0.38
RAFL09-15-A20	Shaggy-like kinase	3.17	0.18
RAFL05-04-D14	Putative protein contains similarity to MYB-like DNA-binding protein	3.03	0.18

*See Table 2 for explanation.

Table 4. Genes up-regulated by both HL and drought*

Clone name	Gene	HL 3 h		Dry 2 h		Dry 5 h	
		Ratio	SD	Ratio	SD	Ratio	SD
RAFL08-13-F10	Putative protein	40.34	17.98	14.94	7.99	27.13	11.50
RAFL06-13-J20	*LEA76* homolog type 1	34.58	5.84	41.79	32.69	51.69	25.54
RAFL07-11-M21*	*RD29A*	21.06	4.89	21.17	5.26	19.01	4.72
RAFL05-04-J20	Nonspecific lipid-transfer protein precursor	20.61	3.20	1.61	0.37	11.12	2.78
RAFL05-18-I12	Unknown protein	14.94	6.70	26.67	12.46	39.80	25.75
RAFL07-07-J02	*AtHVA22d*	14.31	1.05	15.66	5.08	4.85	2.23
RAFL05-05-G20	Unknown protein similar to pollen coat protein	13.97	2.58	4.78	2.58	10.59	4.20
RAFL08-16-M12	*RD20*	10.42	3.54	28.51	12.14	24.36	3.35
RAFL05-19-O22	Unknown protein	9.96	2.72	19.01	9.36	25.72	13.47
RAFL05-08-P17*	*ERD10*	9.46	1.84	16.21	1.90	12.77	7.13
RAFL05-21-F13*	Unknown protein	9.44	1.78	12.73	3.07	22.82	7.65
RAFL05-14-E16*	Putative flavin-containing mono-oxygenase	8.67	0.25	4.85	3.20	13.38	6.24
RAFL06-08-N16*	*KIN1*	8.45	0.76	6.16	4.05	7.98	3.10
RAFL08-11-C23	Late embryogenesis abundant protein *LEA*-like	7.96	4.67	13.06	17.75	6.38	3.20
RAFL05-03-A05*	*COR15a*	7.34	2.47	5.55	1.54	9.34	3.48
RAFL05-11-I09	*RD29B*	6.81	5.22	27.19	19.31	38.39	20.08
RAFL09-06-B11	Putative fatty acid elongase 3-ketoacyl-CoA synthase	6.71	0.96	3.18	1.27	5.23	1.65
RAFL06-10-C16	Unknown protein	6.42	1.64	6.37	6.18	20.24	13.55
RAFL08-12-D11	Putative katanin	6.14	1.32	2.28	0.77	3.23	0.84
RAFL07-14-O18	Putative ripening-related protein	6.10	2.54	4.49	2.40	2.73	0.95
RAFL05-20-N18	*COR15b*	6.08	0.97	3.67	0.98	2.74	0.49
RAFL06-08-H20	*RAP2.6*	5.91	1.30	9.19	7.20	21.72	10.30
RAFL05-14-G18	MtN19-like protein	5.91	0.65	5.12	1.38	6.68	2.13
RAFL08-18-N19	Arabinogalactan-protein (AGP2)	5.69	0.94	5.10	2.03	13.60	5.70
RAFL08-11-D22	Putative stress-related protein	5.69	0.55	2.22	0.95	3.93	1.89
RAFL05-17-B13*	Putative desiccation-related protein *LEA14*	5.60	0.17	12.34	3.15	13.79	5.17
RAFL08-08-L20	Putative galactinol synthase	5.57	0.86	7.51	3.92	6.06	2.36
RAFL05-12-N10	Hypothetical protein	5.52	3.57	3.90	0.74	8.27	3.46
RAFL04-20-N09	*RD17*/*COR47*	5.51	2.12	9.44	1.54	9.06	3.51
RAFL06-15-O23	Polygalacturonase PG1	5.33	1.75	5.24	3.95	4.70	2.14
ERD7*	*ERD7*	5.24	1.83	6.92	6.22	3.16	0.91
RAFL07-07-G15	NAC domain protein	5.22	0.52	7.77	2.00	4.28	1.19
RAFL06-12-J05	Hypothetical protein	5.17	0.71	4.31	2.16	3.26	0.79
RAFL05-16-H23	Putative DNA-binding protein	5.08	1.37	37.77	25.85	8.47	3.30
RAFL05-14-E15	Putative cinnamoyl-CoA reductase	4.91	0.82	2.88	0.64	7.48	2.91
RAFL05-03-I09	*RAB18*	4.83	0.50	4.48	2.99	10.09	4.38
RAFL05-10-H11	Hypothetical protein	4.62	0.60	3.23	1.40	2.31	0.77
RAFL05-10-J09*	Unknown protein	4.59	1.45	21.70	7.06	7.77	2.89
RAFL09-06-L09	Heat shock protein 70	4.54	0.22	1.21	0.36	4.03	1.79
RAFL05-12-N20	Cinnamoyl-CoA reductase-like protein	4.43	1.44	6.21	3.84	5.75	2.03
RAFL05-21-C17	*RD26*	4.32	0.78	12.73	9.58	8.51	4.45
RAFL08-17-O07	Glutathione S-transferase 103-1A	4.19	0.29	4.58	3.28	2.63	0.77
RAFL08-11-P07*	Hypothetical protein	4.16	1.44	7.55	5.13	7.77	3.24
RAFL05-05-E05	Glutathione S-transferase (*GST6*)	4.04	0.26	2.35	0.66	3.17	0.86
ERD9	*ERD9* (glutathione S-transferase)	3.98	0.96	3.26	2.67	1.81	0.63
RAFL05-15-A16	Putative spermidine synthase	3.95	1.51	2.02	0.87	3.89	1.22
RAFL08-11-G23	Putative protein	3.93	0.38	3.33	2.37	3.41	1.79
RD22	*RD22* (ABA-inducible gene)	3.90	1.05	2.94	0.73	4.61	1.62
RD28	*RD28* (water channel protein)	3.82	0.79	10.51	3.01	2.45	0.71
RAFL04-17-M22	Hypothetical protein	3.81	1.95	11.45	4.35	4.52	1.99
RAFL04-18-F11	Lipid transfer protein, glossy 1 homolog	3.75	0.46	4.86	2.53	3.46	1.33
RAFL05-11-E20	Putative acyl-CoA synthetase	3.69	1.46	2.08	0.70	3.12	1.00
RAFL05-07-D07	Kinesin-like calmodulin-binding protein	3.61	0.07	4.09	1.18	3.16	0.92
RAFL09-12-O21	Membrane channel-like protein	3.59	0.41	4.79	1.77	2.04	0.59
RAFL05-14-D05	Putative protein	3.51	0.26	6.43	3.71	4.94	1.95
RAFL06-10-I08	Putative protein	3.49	0.19	3.26	1.35	4.13	1.93
RAFL07-18-P17	Putative protein	3.46	0.96	3.05	0.34	1.98	0.78
RAFL08-10-O05	Expressed protein	3.46	0.76	3.43	2.18	2.25	1.10
AtNCED3	9-*cis*-Epoxycarotenoid dioxygenase	3.44	0.79	16.10	15.18	5.24	0.20
RAFL05-09-N10	Putative protein	3.31	0.91	1.87	0.56	7.11	2.12
RAFL05-16-F03	*En*/*Spm*-like transposon protein	3.28	0.39	17.04	20.33	10.03	6.52
RAFL08-17-D17	Nodulin/glutamate-ammonia ligase-like protein	3.28	0.74	5.43	2.75	4.12	1.72
RAFL06-13-K18	Putative protein	3.24	0.69	4.49	2.87	3.74	1.56
RAFL05-03-K03	Hypothetical protein	3.21	0.19	7.53	2.16	4.39	1.52
RAFL05-10-D11	Lysophospholipase homolog	3.15	0.48	3.96	1.34	3.33	1.64
RAFL11-01-J18	Homeobox-leucine zipper protein *ATHB-12*	3.10	0.62	12.56	6.04	8.31	2.60

Table 4. *Continued*

Clone name	Gene	HL 3 h		Dry 2 h		Dry 5 h	
		Ratio	SD	Ratio	SD	Ratio	SD
RAFL05-16-I09	Sucrose-UDP glucosyltransferase	3.08	0.39	1.62	0.59	4.53	1.56
RAFL05-16-H03	Probable cytochrome P450	3.05	0.45	5.17	2.05	2.29	0.71
RAFL06-09-N04	Putative protein	3.04	0.28	1.49	0.38	4.91	0.99
RAFL05-09-G08	*LEA76* homolog type2	3.03	0.27	6.74	3.73	18.72	11.71
RAFL04-14-P24	Putative cinnamyl alcohol dehydrogenase	3.03	0.08	4.67	1.03	7.04	2.32
RAFL05-04-D14	MYB homolog	3.03	0.18	3.41	0.53	2.42	0.63

*Gene name and corresponding response (ratio) to HL and drought together with the standard deviation (SD) are shown. It should be mentioned that plant age and the harvested tissue are not exactly the same in the HL and drought samples.
†Genes induced by cold and high-salinity stresses (9).

that fibrillins are inducible by HL stress may suggest that the plastoglobule has a role in the protection of chloroplasts against HL stress. Lipid-transfer proteins may have a function in the repair of stress-induced damage in membranes or changes in the lipid composition of membranes (22). Most of the other stress-related genes are thought to be involved in the protection of cellular components (9,23).

Because a number of drought-responsive genes were found among the HL-inducible genes listed in Table S1, we decided to analyze the cross talk between HL and drought responses. In our previous study, response to drought stress was investigated using the same RIKEN cDNA microarray system (9). In this study, the threshold for positive response was reset as more than three-fold induction by the stresses. This analysis revealed an overlap between the two stresses as shown in Fig. 5. Surprisingly, two-thirds of the HL-upregulated genes were also activated by drought stress, demonstrating a dense overlap of the two stresses. The list of genes induced by both stresses is shown in Table 4. The overlap predicts a common signaling pathway for HL and drought responses.

One possible common consequence of these two stresses is an imbalance in the light and dark reactions of photosynthesis. Drought stress causes stomata closure and leads to CO_2 limitation (24). CO_2 limitation is known to cause some HL responses even under moderate light conditions (25), suggesting that an imbalance of the light and dark reactions due to specific enhancement of the former is one of the causes of HL stress. Another common feature between the two stresses is the involvement of ROS. A key regulator of drought response, *DREB2A*, is induced by hydrogen peroxide (26). Hydrogen peroxide is produced under HL conditions, and it is an inducer of one of the HL-inducible genes, *APX2* (27). Therefore, CO_2 limitation or ROS (or both) might lead to activation of the HL- and drought-inducible genes, as shown in Table 4.

Comparison with cold stress-responsive and high-salinity stress-responsive genes (9) identified 10 genes that are upregulated by any of the HL, drought, cold and high-salinity stresses (clones with asterisk, Table 4). These include *RD29A, ERD7, ERD10, KIN1, COR15a* and *LEA14*. This comparison revealed a class of general antistress factors that respond to a broad range of abiotic stresses. Among them, ERD10 and LEA14 belong to the LEA protein family and are involved in the protection of macromolecules such as enzymes and lipids (9,23). *KIN1* may have the ability to neutralize ice nucleators (22). COR15a is a chloroplast-targeted protein and suppresses photoinhibition under cold stress, possibly through stabilization of membranes (28). Although their exact biochemical function is not known, RD29A, ERD10, KIN1, COR15a and LEA1 are all supposed to be involved in the protection of cellular components such as proteins and membranes. Therefore, it would be reasonable for plants to activate factors for cellular protection regardless of the type of abiotic stress.

Genes down-regulated by HL

Thirty genes showed down-regulation by HL stress, and they are listed in Table S4. Interestingly, about half of them are related to the photosynthetic electron transport system (ETS).

Table 5 summarizes the responses of photosynthesis-related genes to HL. Among them, only *ELIP2* was activated. ELIP is a chlorophyll-binding thylakoid protein and is thought to have a role as an antistress factor rather than a light-harvesting component (29). *OHP* is also assumed to have roles similar to those of *ELIP* (29), and *PsbS* has been revealed to be necessary for light energy dissipation (30). Although they did not respond to HL under our experimental conditions, no down-regulation was observed. In contrast, light-harvesting members of the *CAB* superfamily (*Lhca* and *Lhcb* genes) showed the strongest reduction in the transcript level among those responsible for components of ETS. Down-regulation of several antenna genes has been reported previously (5). It should be mentioned that the cDNA microarray system allows cross-hybridization to some extent, so that it is not good at evaluation of individual gene copies with very high homology. The genes for photosystem I, photosystem II and the cytochrome b_6/f complex showed relatively moderate reduction compared with the antenna components. Interestingly, ferredoxin (*petF*) and ferredoxin–$NADP^+$ reductase (*petH*), both of which are terminal components of ETS, showed the least suppression by HL among the genes involved in ETS.

Dose response and kinetics

To confirm using another method the response of the HL-inducible genes revealed by the microarray experiments, quantitative RT-PCR was performed. Figure 6A shows RT-PCR products of the genes that showed positive responses to a treatment of 150 W m^{-2} (*ca* 800 μE m^{-2} s^{-1}) for 3 h, as identified by the microarray analysis. The PCR products in the figure showed the expected product sizes, and these bands were subjected to quantitative analysis. As shown in Fig. 6B, all the analyzed genes showed similar profiles for the kinetic response. Figure 6C shows the responses to several light intensities after 3 h treatments, and the

Table 5. Response to HL of photosynthesis-related genes*

Clone name	Gene	Ratio	SD	MIPS
Photosystem I				
RAFL11-02-M05	*psaE1*	1.04	0.11	At4g28750
RAFL06-08-B20	*petH2*	0.89	0.01	At5g66190
RAFL08-19-M09	*petH1*	0.89	0.12	At1g20020
RAFL06-14-F04	ferredoxin	0.81	0.04	At4g14890
RAFL05-18-N22	*petF1*	0.73	0.07	At1g60950
RAFL06-07-K01	*psaL*	0.44	0.05	At4g12800
RAFL04-19-B03	*psaH2*	0.42	0.02	At3g16140
RAFL06-08-M21	*psaN*	0.41	0.02	At5g64040
RAFL09-06-G16	*psaF*	0.35	0.04	At1g31330
RAFL05-04-D24	*psaH1*	0.33	0.02	At1g52230
RAFL05-01-P13	*psaD1*	0.31	0.04	At4g02770
Photosystem II				
RAFL05-18-I22	*psbS*	1.74	0.12	At1g44575
RAFL05-17-F20	*psbR*	0.55	0.08	At1g79040
RAFL05-17-B17	*psbO2*	0.53	0.03	At3g50820
RAFL05-01-G05	*psbW*	0.49	0.05	At2g30570
RAFL05-17-G17	*psbQ1*	0.42	0.01	At4g21280
RAFL08-19-L15	*psbT1*	0.39	0.03	At3g21050
RAFL06-16-A22	oee enhancer 3	0.28	0.05	At4g05180
RAFL05-04-A19	*psbT2*	0.25	0.02	At1g51400
Cytochrome b_6/f complex				
RAFL05-03-B18	*petM*	0.49	0.05	At2g26500
ATPase complex				
RAFL06-07-K18	*atpD*	0.79	0.04	At4g09650
RAFL04-17-B14	*atpG*	0.67	0.09	At4g32260
CAB superfamily				
RAFL04-12-M20	*ELIP2*	22.53	10.80	At4g14690
RAFL06-08-F19	*OHP*	1.04	0.07	At5g02120
RAFL04-17-G15	*Lhcb1.1*	0.57	0.05	At1g29920
RAFL09-06-C02	*Lhca3*	0.44	0.10	At1g61520
RAFL06-12-K03	*Lhca1*	0.33	0.02	At3g54890
RAFL02-10-L11	*Lhcb3*	0.33	0.05	At5g54270
RAFL05-11-O16	*Lhca2*	0.33	0.01	At3g61470
RAFL06-14-A20	*Lhca4*	0.32	0.03	At3g47470
RAFL04-14-C14	*Lhcb2.1*	0.32	0.07	At2g05100
RAFL05-21-O22	*Lhcb1.4*	0.31	0.03	At2g34420
RAFL06-10-O24	*Lhcb6*	0.27	0.02	At1g15820
RAFL05-11-L07	*Lhcb2.3*	0.27	0.01	At3g27690
RAFL06-09-H06	*Lhcb1.3*	0.25	0.02	At1g29910
RAFL09-07-C06	*Lhcb1.5*	0.21	0.03	At2g34430
RAFL08-10-P13	*Lhcb1.2*	0.19	0.03	At1g29930
RAFL06-09-F16	*Lhcb4.2*	0.19	0.02	At3g08940
RbcS				
RAFL06-14-L16	*Rbcs1b*	0.95	0.46	At5g38430
RAFL06-08-L09	*RbcS2b*	0.66	0.03	At5g38420
RAFL04-15-J15	*RbcS3b*	0.57	0.05	At5g38410

*See Table 2 for explanation.

relative mRNA amounts are indicated. Among the analyzed genes, three genes (RAFL09-06-O18, RAFL04-09-J20 and RAFL04-12-M20) showed saturated responses below 350 W m^{-2} (*ca* 1800 μE m^{-2} s^{-1}), whereas the other genes showed their highest responses at 350 W m^{-2}. Because there had been no report on dose–response relationship for HL-dependent gene expression, this result is the first demonstration of saturated light intensities for the activation of HL-inducible genes in plants. The multiple types of response revealed may suggest that there are differential mechanisms for induction by HL.

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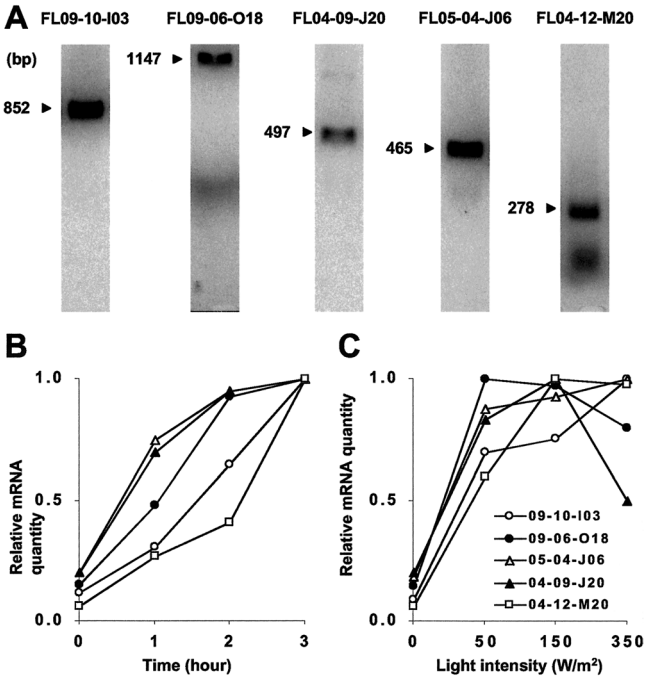

Figure 6. Expression profiles of several HL-inducible genes revealed by quantitative RT-PCR analysis. A: Identification of the RT-PCR products. RT-PCR products were stained with VistraGreen and separated by gel electrophoresis, and fluorescence images of the products are shown. Arrowhead indicates the position of the corresponding gene products. Sizes of the products shown in the figure are the expected PCR products calculated using the gene structure and position of the primers. B and C: relative mRNA amounts determined by quantitative RT-PCR. Quantification of mRNA amount was carried out with the aid of a series of diluted samples. B: Time course of the HL response. Seedlings were illuminated with 150 W m^{-2} for the indicated periods and the relative mRNA amount was analyzed. Symbols for genes in the graph are the same as for Fig. 1C. C: Dose response to light intensity. Seedlings were illuminated with the indicated intensities for 3 h, and the relative mRNA amount was analyzed.

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Table S1. List of up-regulated genes by HL stress

Clone Name	Gene	Ratio	SD	MIPS
RAFL08-13-F10	putative protein	40.34	17.98	At5g03210
RAFL06-13-J20	LEA76 homologue type 1	34.58	5.84	At1g52690
RAFL04-12-M20	ELIP2	22.53	10.80	At4g14690
RAFL07-11-M21	RD29A	21.06	4.89	At5g52310
RAFL05-04-J20	nonspecific lipid-transfer protein precursor	20.61	3.20	At5g59320
RAFL05-18-I12	unknown protein	14.94	6.70	At2g47770
RAFL07-07-J02	AtHVA22d	14.31	1.05	At4g24960
RAFL05-05-G20	unknown protein similar to pollen coat protein	13.97	2.58	At3g02480
RAFL09-06-F09	putative nonspecific lipid-transfer protein precursor	12.35	0.76	At5g59310
RAFL08-16-M12	RD20 (putative Ca2+-binding EF-hand protein)	10.42	3.54	At2g33380
RAFL09-09-N16	flavanone 3-hydroxylase (F3H)	10.22	2.18	At3g51240
RAFL05-19-O22	unknown protein	9.96	2.72	At3g03310
RAFL05-08-P17	Dehydrin ERD10 (Low-temperature-induced protein LTI45)	9.46	1.84	At1g20450
RAFL05-21-F13	Unknown protein	9.44	1.78	At1g16850
RAFL11-09-C12	metallothionein-like protein 1a (MT1a)	9.34	3.41	At1g07600
RAFL05-14-E16	putative flavin-containing monooxygenase	8.67	0.25	At1g62570
RAFL06-08-N16	KIN1	8.45	0.76	At5g15960
RAFL08-11-C23	late embryogenesis abundant protein LEA like	7.96	4.67	At5g06760
RAFL11-11-C18	protein serine/threonine kinase-like protein	7.73	3.90	At5g10290
RAFL09-06-P19	putative fibrillin	7.67	2.19	At4g04020
RAFL05-03-A05	cold-regulated protein cor15a precursor	7.34	2.47	At2g42540
RAFL05-11-I09	RD29B	6.81	5.22	At5g52300
RAFL09-06-B11	putative fatty acid elongase 3-ketoacyl-CoA synthase	6.71	0.96	At1g07720
RAFL06-10-C16	unknown protein	6.42	1.64	At1g05340
RAFL08-12-D11	putative katanin	6.14	1.32	At2g34560
RAFL07-14-O18	putative ripening-related protein	6.10	2.54	At5g59480
RAFL05-20-N18	cold-regulated protein cor15b precursor	6.08	0.97	At2g42530
RAFL06-08-H20	RAP2.6	5.91	1.30	At1g43160
RAFL05-14-G18	MtN19-like protein	5.91	0.65	At5g61820
RAFL08-18-N19	arabinogalactan-protein (AGP2)	5.69	0.94	At2g22470
RAFL08-11-D22	putative stress related protein	5.69	0.55	At1g67360
RAFL05-17-B13	putative desication related protein LEA14	5.60	0.17	At1g01470
RAFL08-08-L20	putative galactinol synthase	5.57	0.86	At1g56600
RAFL05-12-N10	hypothetical protein	5.52	3.57	At2g37870
RAFL04-20-N09	RD17/COR47	5.51	2.12	At1g20440
RAFL06-15-O23	polygalacturonase PG1like	5.33	1.75	At1g48100
ERD7	ERD7	5.24	1.83	At2g17840

RAFL07-07-G15	NAC domain protein	5.22	0.52	At1g01720
RAFL06-12-J05	hypothetical protein	5.17	0.71	At1g56580
RAFL05-16-H23	putative DNA-binding protein	5.08	1.37	At4g28140
RAFL05-12-M18	Putative L-ascorbate peroxidase, chloroplast precursor (Thylakoid lumenal 29 kDa protein) (TL29) (P29)	5.04	0.54	At4g09010
RAFL05-14-E15	putative cinnamoyl-CoA reductase	4.91	0.82	At2g33590
RAFL07-09-L01	S-adenosyl-L-homocystein hydrolase	4.85	0.72	At3g23810
RAFL05-03-I09	RAB18	4.83	0.50	At5g66400
RAFL04-09-J20	NaCl-inducible Ca2+-binding protein-like	4.74	0.61	At5g49480
RAFL08-09-F22	hypothetical protein	4.63	0.63	At1g61890
RAFL05-10-H11	hypothetical protein	4.62	0.60	At2g21810
RAFL05-10-J09	unknown protein	4.59	1.45	At1g78070
RAFL09-06-L09	heat shock protein 70	4.54	0.22	At3g12580
RAFL05-12-N20	cinnamoyl-CoA reductase - like protein	4.43	1.44	At4g30470
RAFL08-08-L21	SIG5	4.41	1.34	At5g24120
RAFL05-21-C17	RD26	4.32	0.78	At4g27410
RAFL07-15-H10	putative protein	4.31	0.83	At3g56290
RAFL04-12-P04	probable squalene monooxygenase	4.19	0.64	At5g24150
RAFL08-17-O07	Glutathione S-transferase 103-1A	4.19	0.29	At2g29450
RAFL08-11-P07	hypothetical protein	4.16	1.44	At5g17460
RAFL09-15-O19	hypothetical protein	4.09	0.94	At4g09810
RAFL07-08-K14	At-hsc70-3	4.04	0.34	At3g09440
RAFL05-05-E05	glutathione S-transferase (GST6)	4.04	0.26	At2g47730
RAFL04-17-B12	cold-regulated protein COR6.6 (KIN2)	4.02	0.24	At5g15970
ERD9	ERD9 (glutathione S-transferase)	3.98	0.96	At1g10360
RAFL05-15-A16	putative spermidine synthase	3.95	1.51	At5g53120
RAFL08-11-G23	putative protein	3.93	0.38	At3g63060
RAFL05-07-A03	putative lemir (miraculin) protein	3.93	1.20	At1g17860
RAFL08-15-C22	squalene epoxidase - like protein	3.93	0.35	At4g37760
RD22	RD22 (ABA inducible gene)	3.90	1.05	At5g25610
RAFL07-13-H08	heat shock protein 90	3.84	0.57	At5g56010
RD28	RD28 (water channel protein)	3.82	0.79	At2g37170
RAFL04-18-F22	putative protein	3.81	0.19	At5g42760
RAFL04-17-M22	hypothetical protein	3.81	1.95	At1g73380
RAFL04-18-F11	lipid transfer protein; glossy1 homolog	3.75	0.46	At5g57800
RAFL09-16-A18	unknown protein	3.71	0.27	At2g45620
RAFL08-13-J12	unknown protein	3.71	0.77	At3g17800
RAFL05-11-E20	putative acyl-CoA synthetase	3.69	1.46	At2g04350
RAFL08-16-O05	glucose-1-phosphate adenylyltransferase (APL3)	3.65	0.78	At4g39210
RAFL08-13-O15	putative galactinol synthase	3.64	1.70	At2g47180
RAFL05-07-D07	kinesin-like calmodulin-binding protein	3.61	0.07	At5g65930
RAFL09-16-P08	putative glutathione reductase	3.60	0.84	At3g24170
RAFL09-12-O21	membrane channel-like protein	3.59	0.41	At4g17340
RAFL06-12-A20	putative RING-H2 zinc finger protein	3.53	0.38	At1g15100
RAFL09-10-I03	chalcone synthase	3.53	0.51	At5g13930
RAFL05-14-D05	putative protein	3.51	0.26	At4g21570
RAFL06-10-I08	putative protein	3.49	0.19	At5g50100

RAFL07-18-P17	putative protein	3.46	0.96	At5g20070
RAFL08-10-O05	expressed protein	3.46	0.76	At1g80110
AtNCED3	9-cis-epoxycarotenoid dioxygenase	3.44	0.79	At1g78390
RAFL09-07-E08	myb family protein	3.37	0.85	At4g21440
RAFL05-09-N10	putative protein	3.31	0.91	At3g57010
RAFL05-16-F03	En/Spm-like transposon protein	3.28	0.39	At1g49450
RAFL08-17-D17	nodulin / glutamate-ammonia ligase - like protein	3.28	0.74	At3g53180
RAFL06-13-K18	putative protein	3.24	0.69	At3g62260
RAFL09-15-D20	putative cold acclimation protein	3.22	0.51	At3g50830
RAFL05-13-B03	putative protein	3.21	0.45	At5g43850
RAFL05-03-K03	hypothetical protein	3.21	0.19	At4g25670
RAFL09-15-A20	shaggy-like protein kinase iota	3.17	0.18	At1g06390
RAFL04-17-J19	putative fructose-2,6-bisphosphatase	3.15	0.72	At1g07110
RAFL05-10-D11	lysophospholipase homolog	3.15	0.48	At1g73480
RAFL04-18-D20	Similar to dTDP-D-glucose 4,6-dehydratase	3.13	0.04	At1g78570
RAFL09-06-O18	HEAT SHOCK PROTEIN 81-2 (HSP81-2)	3.11	0.35	At5g56030
RAFL11-01-J18	homeobox-leucine zipper protein ATHB-12	3.10	0.62	At3g61890
RAFL08-19-G11	At14a	3.09	0.27	At3g28270
RAFL05-04-J06	Probable phospholipid hydroperoxide glutathione peroxidase (PHGPx) (AtGPX1)	3.08	0.48	At4g11600
RAFL05-16-I09	sucrose-UDP glucosyltransferase	3.08	0.39	At5g20830
RAFL07-12-B04	mannan endo-1,4-beta-mannosidase	3.05	0.22	At5g66460
RAFL05-16-H03	probable cytochrome P450	3.05	0.45	At4g00360
RAFL06-09-N04	putative protein	3.04	0.28	At5g48180
RAFL05-09-G08	LEA76 homologue type2	3.03	0.27	At3g15670
RAFL04-14-P24	putative cinnamyl alcohol dehydrogenase	3.03	0.08	At4g34230
RAFL05-04-D14	MYB homolog	3.03	0.18	At5g67580
RAFL08-12-I18	putative alcohol dehydrogenase	3.02	0.62	At2g37760

Table S2 Response of detoxification enzymes to HL stress

Clone Name	Gene	Ratio	SD	MIPS
RAFL05-12-M18	Putative L-ascorbate peroxidase, chloroplast precursor (Thylakoid lumenal 29 kDa protein) (TL29) (P29)	5.04	0.54	At4g09010
RAFL08-17-O07	Glutathione S-transferase 103-1A (GST 103-1A)	4.19	0.29	At2g29450
RAFL05-05-E05	glutathione S-transferase (GST6)	4.04	0.26	At2g47730
ERD9	glutathione S-transferase (ERD9)	3.98	0.96	At1g10360
RAFL09-16-P08	putative glutathione reductase (GR h)	3.60	0.84	At3g24170

RAFL05-04-J06	Probable phospholipid hydroperoxide glutathione peroxidase (PHGPx) (AtGPX1)	3.08	0.48	At4g11600
RAFL05-02-I23	putative ascorbate peroxidase (APX	2.46	0.18	At1g07890
RAFL05-13-J04	catalase (CAT2)	2.22	0.24	At4g35090
RAFL08-10-N15	putative stromal ascorbate peroxidase (sAPX)	1.89	0.09	At4g08390
RAFL07-07-K13	putative monodehydroascorbate reductase (MDAR h1)	1.41	0.64	At1g63940
RAFL03-07-O21	putative GSH-dependent dehydroascorbate reductase (GSH-DHAR h)	1.39	0.12	At1g19570
RAFL05-15-H10	glutathione S-transferase (GST18)	1.38	0.03	At2g02390
RAFL05-10-E23	putative monodehydroascorbate reductase (MDAR h2)	1.33	0.18	At3g27820
RAFL05-16-O07	glutathione S-transferase (GST)	1.32	0.26	At1g02930
RAFL06-10-P23	putative ascorbate peroxidase (APX	1.25	0.15	At4g35000
RAFL05-18-K12	putative glutathione transferase (GST h1)	1.10	0.04	At1g78370
RAFL08-12-A04	copper/zinc superoxidase dismutase (CSD1)	1.10	0.06	At1g08830
RAFL05-12-D11	glutathione transferase (GST 10)	1.09	0.08	At5g41210
RAFL06-10-G18	GLUTATHIONE S-TRANSFERASE (ERD13)	1.00	0.10	At2g30870
RAFL04-10-C01	glutathione transferase-like protein (GST h2)	0.95	0.07	At3g43800
RAFL05-14-B03	manganese superoxide dismutase (MSD1)	0.89	0.06	At3g10920
RAFL03-05-I07	Glutathione S-transferase (PM24)	0.74	0.11	At4g02520

Table S3. Response of the phenylpropanoid pathway to HL stress

Clone Name	Gene	Ratio	SD	MIPS
RAFL09-09-N16	flavanone 3-hydroxylase (F3H)	10.22	2.18	At3g51240
RAFL05-14-E15	putative cinnamoyl-CoA reductase (CCR h1)	4.91	0.82	At2g33590
RAFL05-12-N20	cinnamoyl-CoA reductase - like protein (CCR h2)	4.43	1.44	At4g30470
RAFL09-10-I03	chalcone synthase (CHS)	3.53	0.51	At5g13930
RAFL04-14-P24	putative cinnamyl alcohol dehydrogenase (CAD h1)	3.03	0.08	At4g34230
RAFL04-17-C19	probable caffeoyl-CoA O-methyltransferase (CCoAOMT h)	2.89	0.15	At4g34050
RAFL05-18-A06	putative cinnamyl alcohol dehydrogenase (CAD h2)	2.73	0.84	At1g09500
RAFL04-17-E23	cinnamyl alcohol dehydrogenase 2 (CAD2)	2.35	0.25	At3g19450

RAFL06-07-M15	O-methyltransferase (OMT)	2.21	0.23	At5g54160
RAFL04-16-O21	putative flavanone 3-hydroxylase (F3H h)	1.67	0.39	At5g24530
RAFL06-09-K20	putative leucoanthocyanidin dioxygenase (LDOX h1)	1.46	0.20	At4g22880
RAFL05-03-O21	leucoanthocyanidin dioxygenase-like protein (LDOX h2)	1.45	0.34	At5g05600
RAFL05-09-D14	phenylalanine ammonia lyase (PAL1)	1.35	0.15	At2g37040
RAFL06-16-E14	putative cinnamyl alcohol dehydrogenase (CAD h3)	1.35	0.40	At1g09490
RAFL09-06-C22	4-coumarate-CoA ligase-like protein (4CL h)	1.28	0.17	At3g48990
RAFL04-16-D08	phenylalanine ammonia-lyase 2 (PAL2)	1.14	0.22	At3g53260

Table S4 Down-regulated gened by HL stress

Clone Name	Gene	Ratio	SD	MIPS
RAFL05-01-A07	unknown protein	0.10	0.01	At3g15450
RAFL06-09-F16	Lhcb4.2	0.19	0.02	At3g08940
RAFL08-10-P13	Lhcb1.2	0.19	0.03	At1g29930
RAFL09-07-C06	Lhcb1.4	0.21	0.03	At2g34430
RAFL11-02-D19	unknown protein	0.21	0.02	At2g45180
RAFL05-02-K03	putative light regulated protein	0.22	0.03	At3g26740
RAFL06-15-F04	unknown protein	0.23	0.03	At1g10500
RAFL04-15-D02	vegetative storage protein-like	0.23	0.00	At5g44020
RAFL06-08-D09	unknown protein	0.25	0.04	At2g10940
RAFL06-09-H06	Lhcb1.3	0.25	0.02	At1g29910
RAFL05-04-A19	psbT2	0.25	0.02	At1g51400
RAFL05-01-M12	putative dormancy-associated protein	0.26	0.04	At1g28330
RAFL07-11-I06	putative protein	0.27	0.05	At5g11420
RAFL05-11-L07	Lhcb2.3	0.27	0.01	At3g27690
RAFL04-18-L04	putative alcohol dehydrogenase	0.27	0.03	At1g64710
RAFL06-10-O24	Lhcb6	0.27	0.02	At1g15820
RAFL05-02-P09	putative protein	0.28	0.04	At4g27450
RAFL04-13-K03	putative aluminium-induced protein	0.29	0.03	At5g19140
RAFL06-09-P22	delta tonoplast integral protein (delta-TIP)	0.29	0.04	At3g16240
RAFL08-09-D04	unknown protein	0.31	0.03	At2g39570
RAFL04-09-O24	putative xyloglucan endo-1,4-beta-D-glucanase precursor	0.31	0.03	At4g30270
RAFL06-11-I04	putative protein	0.31	0.05	At4g35750
RAFL05-21-O22	Lhcb1.5	0.31	0.03	At2g34420
RAFL05-01-P13	psaD1	0.31	0.04	At4g02770
RAFL04-14-C14	Lhcb2.1	0.32	0.07	At2g05100
RAFL07-16-B09	putative protein	0.32	0.06	At3g48360
RAFL05-04-M01	E2, putative ubiquitin-conjugating enzyme	0.32	0.02	At1g64230

RAFL05-11-O16	Lhca2	0.33	0.01	At3g61470
RAFL02-10-L11	Lhcb3	0.33	0.05	At5g54270
RAFL05-04-D24	psaH1	0.33	0.02	At1g52230
RAFL06-12-K03	Lhca1	0.33	0.02	At3g54890