PHOTOSYNTHETICA 43 (2): 231-236, 2005

Genes differentially expressed under photoinhibition stress in flag leaves of super-hybrid rice Liangyoupeijiu (*Oryza sativa*) and their genetic origins

G.-Q. JIANG[*,**], J.-L. GUO[*,***], Q.-W. MENG[**], Y.-Q. CHEN[***], H.-X. WANG[*], Z.-A. HU[*,+] ,
and T.-Y. KUANG[*]

Key Laboratory of Photosynthesis and Molecular Physiology, Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun 100093, Beijing, P.R. China[*]
College of Life Sciences, Shandong Agricultural University, Tai'an 271018, Shandong, P.R. China[**]
College of Bioengineering, Fujian Normal University, Fuzhou 350007, Fujian, P.R. China[***]

Abstract

Genes differentially expressed under high irradiance (HI) stress in mature flag leaves of super-hybrid rice Liangyoupeijiu (*Oryza sativa* ssp. *indica*) were studied by the silver-staining mRNA differential display technique. We obtained 167 differentially displayed bands on silver-stained polyacrylamide gels and searched for their genetic origins. Five cDNA fragments, which were upregulated by HI stress, were cloned and sequenced. The clones of G25×320, A31×380, and G29×280 putatively encode a cytosolic monodehydroascorbate reductase (MDAR), a phosphatidylinositol 4-kinase (PI-4-K), and a DEAH-box RNA helicase, respectively. Most differentially expressed genes in hybrid rice were inherited from parents and many of them were related with both parents, although some were derived from one parent only. The differentially expressed cDNA fragments having no distinct genetic origins indicated the involvement of some unclear mechanisms in the inheritance processes from parents to hybrid.

Additional key words: cDNA; DDRT-PCR; hybrid rice; Southern blot.

Introduction

Photons, as the energy source for photosynthesis and as an environmental signal for regulating physiological and developmental processes, are one of the prerequisites for plants. Excess photons, however, can lead to photoinhibition, which means decline of radiant energy transfer efficiency and photodamage to the photosynthetic apparatus, and finally leads to lower plant yields (Kok 1956, Powles 1984).

In order to maintain photosynthetic functions under high irradiance (HI) stress, plants have developed various photo-adaptive mechanisms. Excess photons decrease the pH in the thylakoid lumen and develop a transthylakoid pH gradient (Jagendorf 1961). This may favour the aggregation of light-harvesting complex of photosystem 2 (LHC2) particles in the antenna and facilitate a cyclic electron transport depending on photosystem 2 (PS2) to increase thermal dissipation (Horton and Ruban 1992, Whitmarsh *et al.* 1994). And the xanthophyll cycle consisting of the reversible conversion of the diepoxide violaxanthin (V) to the epoxide-free zeaxanthin (Z) *via* the monoepoxide antheraxanthin (A) has been considered the more efficient way to dissipate excess excited energy in thermal forms (Pfündel and Bilger 1994, Demmig-Adams and Adams 1996). Furthermore, the water–water cycle will play dual important roles in scavenging of reactive oxygen species (ROS) and dissipating of excess

---

Received 24 June 2004, *accepted* 13 January 2005.
[+]Author for correspondence; fax: +86 10 62590833, e-mail: huzhiang@ibcas.ac.cn

Abbreviations: A – antheraxanthin; APX – ascorbate peroxidases; CAT – catalases; cysQ – ammonium transport protein; DDRT-PCR – differential display reverse transcription polymerase chain reaction; gyrA – DNA gyrase; HO· – hydroxyl radical; H_2O_2 – hydrogen peroxide; LHC2 – light-harvesting complex of photosystem 2; MDAR – monodehydroascorbate reductase; $^1O_2$ – singlet oxygen; O_2^- – superoxide radical; ORF – open reading-frame; PAR – photosynthetically active radiation; PCR – polymerase chain reaction; PI – phosphatidylinositol; PI-4-K – phosphatidylinositol 4- kinase; PS2 – photosystem 2; RACE – rapid amplification of cDNA ends; ROS – reactive oxygen species; RT-PCR – reverse transcription polymerase chain reaction; SOD – superoxide dismutases; V – violaxanthin; Z – zeaxanthin.

Acknowledgements: We thank Professor De-Mao Jiao from Jiangsu Academy of Agricultural Sciences for offering the seeds and seedlings of super-hybrid rice Liangyoupeijiu and its parents. This research was supported by the State Key Basic Research and Development Plan of China (G1998010100).

excitation energy (Asada 1999). Enzymes such as superoxide dismutases (SOD), ascorbate peroxidases (APX), and catalases (CAT) and molecules including ascorbate, carotenoids, α-tocopherols, anthocyanins, and flavonoids are involved in ROS detoxification in plants (Bohnert and Sheveleva 1998, Niyogi 1999). Moreover, the 32 kDa D1 protein which is encoded by the plastid *psbA* gene is essential for the reaction centre of PS2. Its rapid turnover can effectively prevent the over-damage of the PS2 reaction centre by HI and the D1 protein itself is hypothesized to play a main role in the mechanism of photoinhibition (Long *et al*. 1994, Noam *et al*. 2003).

To date very little is known about the signal transduction pathways under HI stress. However, it is clear that the photoinhibition processes involve the alteration of expression pattern of genes with protective functions. Besides the *psbA* gene coding for the D1 protein, a gene encoding cytosolic ascorbate peroxidase (APX2) is rapidly induced by HI stress (Michael *et al*. 2003). The photo-oxidative stress in the chloroplasts also induced a nuclear gene encoding the plastid protein, fibrillin (Chen *et al*. 1998). In *Arabidopsis thaliana*, five genes, named *Lsr1–Lsr5* (light stress-regulated), were increased drastically in response to irradiance stress. These genes were isolated and identified to encode ERD15 (early responsive to dehydration), ACT2 (actin 2), LEA14 (late embryogenesis abundant), MT1a (metallothionein class 1a), and a novel protein with high similarity to β-1,3-galactosyltransferases from human, respectively (Dunaeva and Adamska 2001). To our knowledge, however, no systematic study on gene expression under photoinhibition in crops has been reported.

In this study, we chose a super-hybrid rice Liangyoupeijiu (*Oryza sativa* ssp. *indica*) and its female parent Peiai 64S and male parent 9311 to study the genes differentially expressed in the hybrid under HI stress and their genetic origins by using silver staining differential display reverse transcription polymerase chain reaction (DDRT-PCR) method (Deng *et al*. 1999).

Materials and methods

Plants and photoinhibition treatment: The seeds of the super-hybrid rice Liangyoupeijiu (*Oryza sativa* ssp. *indica*), its female parent Peiai 64S, and male parent 9311 were surface sterilized in 5 % (m/v) sodium hypochlorite for 20 min, washed intensively with sterilized water, and then soaked in warm water (about 40 °C). The germinated seedlings were planted for 30 d and then transplanted to the pots of 30 cm in height and 25 cm in diameter for 30 d.

Photoinhibition treatment was performed on detached mature flag leaves by floating on water and exposing to HI (2 000 µmol m^{-2} s^{-1} PAR). We measured the irradiance by a *LI-188B* integrating quantum radiometer/photometer (*Li-Cor*, Lincoln, NE, USA) generated by a halogen lamp (Wang *et al*. 2002). Non-photoinhibited controls were put in the greenhouse and the irradiance was about 300 µmol m^{-2} s^{-1} PAR. Plant materials were collected and used either immediately or after being frozen in liquid nitrogen and stored at –70 °C.

Total RNA isolation and DNAase I treatment: Total RNAs were extracted from rice leaves according to the AGPC method (Chomczynski and Sacchi 1987). RNA pellets were dissolved in 97 mm^3 DNAase I buffer and treated with 3 mm^3 RNAase-free DNAase I (*Amersham*, Piscataway, USA) for 1 h at 37 °C. DNAase I was removed by extraction with one volume of phenol/chloroform/iso-amyl alcohol mixture (25 : 24 : 1, v/v/v) and centrifugation at 10 000×*g* for 5 min at 4 °C. Aqueous phases were collected and RNAs were precipitated by 2.5 volume of ethanol at –20 °C for 1 h in presence of 0.1 volume of 3 M sodium acetate (pH 5.2). After centrifuging at 10 000×*g* for 20 min at 4 °C and washing twice with 70 % ethanol, the air-dried RNA pellets were dissolved in TE buffer (10 mM Tris, 1 mM EDTA, pH 8.0).

mRNA differential display: DDRT was conducted according to our previous study (Deng *et al*. 1999) using the anchored primers (HT11M: 5’-AAGCTTTTTTTTTTTA/G/C-3’) and the arbitrary primers listed in Table 1. After denaturation, PCR was carried out for 40 cycles (94 °C for 30 s, 40 °C for 2 min, 72 °C for 30 s) and a final elongation for 5 min at 72 °C. The amplified cDNA fragments were separated on 6 % denaturing polyacrylamide gels using the *Mini-PROTEAN II* electrophoresis cell (*Bio-Rad*, Hercules, USA) and stained by silver staining method.

Table 1. Sequences of the arbitrary primers.

Name	Sequence
HAP25	5’-AAGCTTTCCTGGA-3’
HAP26	5’-AAGCTTGCCATGG-3’
HAP27	5’-AAGCTTCTGCTGG-3’
HAP28	5’-AAGCTTACGATGC-3’
HAP29	5’-AAGCTTAGCAGCA-3’
HAP30	5’-AAGCTTCGTACGT-3’
HAP31	5’-AAGCTTGGTGAAC-3’
HAP32	5’-AAGCTTCCTGCAA-3’

Cloning and sequencing of the differentially expressed cDNA fragments: The fragments were cut out from gels and added to a tube to boil with water for 15 min. The extracts were used as the template to re-amplify the corresponding fragments with the same pair of primers as in PCR. The products of re-amplification were separated on a 0.8 % agarose gel, and the proper bands were cut out and purified by *GFX^{TM}* PCR DNA and Gel Band Purification Kit (*Amersham Pharmacia*, Piscataway, USA). The purified cDNA fragments were cloned using *pGEM-T* Easy Clone Kit (*Promega*, Madison, USA) and transformed into *E. coli* DH5α. They were sequenced using T3 and T7 primers on the *Prism^{TM} 377* DNA Sequencer (*ABI*, Foster City, USA). DNA similarity analysis was conducted by *BLASTN* or by *BLASTX* with current *GenBank* DNA and protein sequences at the *NCBI* website (Altschul *et al*. 1997).

cDNA Southern blot analysis: cDNAs reverse transcribed from RNA samples isolated from the photoinhibited and non-photoinhibited samples from female parent, hybrid, and male parent were denatured before printed onto N$^+$ nylon membrane (*Boehringer Mannheim*, Mannheim, Germany) and fixed for 2 h at 80 °C. The purified DNA fragments of differentially expressed clones were labelled using *Gene Images^{TM}* random primer labelling module (*Amersham Pharmacia*, Little Chalfont, UK) to generate probes for Southern blot hybridization. The detection of hybridization signal was performed using *Gene Images^{TM} CDP-Star* detection module (*Amersham Pharmacia*, Little Chalfont, UK).

Results

Identification of differentially expressed cDNA fragments: In order to identify a whole cluster of genes differentially expressed under HI stress in flag leaves of the hybrid rice Liangyoupeijiu, DDRT-PCR were carried out using 24 combinations of the anchored and arbitrary primers theoretically covering all the possibility of mRNAs. Despite most cDNA bands displayed on the gels showed no alteration of staining intensity among samples, presenting genes not in response to photoinhibition, 167 cDNA fragments differentially expressed in response to HI stress were obtained in total. They could be categorized to four groups according to the their presence (represented by "+" when the corresponding stained bands showed lower intensity, and "++" when the corresponding stained bands showed higher intensity) or absence (represented by "–") in photoinhibited and non-photoinhibitited leaves in the corresponding positions on the silver-stained polyacrylamide gels (Table 2).

Genetic origins of differentially expressed cDNA fragments: The genetic origins of the differentially expressed cDNA fragments under HI stress could be estimated by the bands existing (represented by "+") or not (represented by "–") in the parental strains on silver-stained polyacrylamide gels. The 167 differentially expressed cDNA fragments were categorized to 4 genetic origin types (Table 3).

Table 2. Types of the genes differentially expressed under high irradiance stress in the flag leaves of the hybrid rice.

Gene type	Bands in photoinhibited leaves	non-photoinhibited leaves	Band number	Examples (in Fig. 1)
Genes induced by photoinhibition	+	–	54	a, b, e, h
Genes sensitive to photoinhibition	–	+	41	d
Genes up-regulated by photoinhibition	++	+	45	c, g, i
Genes down-regulated by photoinhibition	+	++	27	f

Table 3. Genetic origin types of the genes differentially expressed under high irradiance stress in the flag leaves of the hybrid rice.

Genetic origin type	Bands in female parent	Bands in male parent	Band number	[%]	Examples (in Fig. 1)
Female parent origin	+	–	26	15.57	e, i
Male parent origin	–	+	33	19.76	d
Bi-parental origin	+	+	68	40.72	a, b, c, f, g
Unclear origin	–	–	40	23.95	h

Identification of the genes up-regulated by HI stress: The cDNA fragments differentially expressed under HI stress were named according to the rule "anchor primer (A, C, or G) – arbitrary primer (25–32) × relative molecular mass". For example, G25×320 represents the cDNA fragment amplified by the anchor primer HT$_{11}$G and the arbitrary primer HAP25 with molecular mass of 320 bp. Five up-regulated cDNA fragments G29×280 (Fig. 2A), A31×380 (Fig. 2*C*), G25×320 (Fig. 2*B*), A31×340 (Fig. 2*C*), and A31×360 (Fig. 2*C*) were selected for cloning and sequencing. The sequences obtained were submitted to *GenBank* and analyzed for similarity using *BLAST* programs.

The G29×280 clone (Accession no. AY189691) was identical to a BAC clone OJ1163_G04 (Accession no. AP003815) of the genomic DNA on chromosome 7 in *O. sativa* ssp. *japonica* which encodes a putative DEAH-box RNA helicase (Accession no. BAC79592). The A31×380 clone (Accession no. AY189692) showed high similarity (99 %) to a genomic ORF sequence located on chromosome 1 (Accession no. AP003735, AAF34418) in *O. sativa* ssp. *japonica* which encodes a putative phosphatidylinositol 4-kinase (PI-4-K) in the hybrid Liangyoupeijiu. The protein encoded by the G25×320 clone (Accession no. AY189693) was identical to a cytosolic monodehydroascorbate reductase (MDAR) in rice. The A31×340 clone (Accession no. AY189694) and the A31×360 clone (Accession no. AY189695) had high similarities (99 %) with ammonium transport protein (cysQ) genes (Accession no. M80795, M55170, *etc.*) and DNA gyrase (gyrA) genes (Accession no. X06373, Y00544, *etc.*), respectively.

cDNA Southern blot analysis: The results of the cDNA Southern blot analyses confirmed that G29×280, A31×380, G25×320, A31×340, and A31×360 were up-regulated by HI stress in hybrid rice (Fig. 3). G29×280 derived from the male parent according to the hybridization signals in parents, A31×360 derived from the female parent, and the remainder derived from both parents.

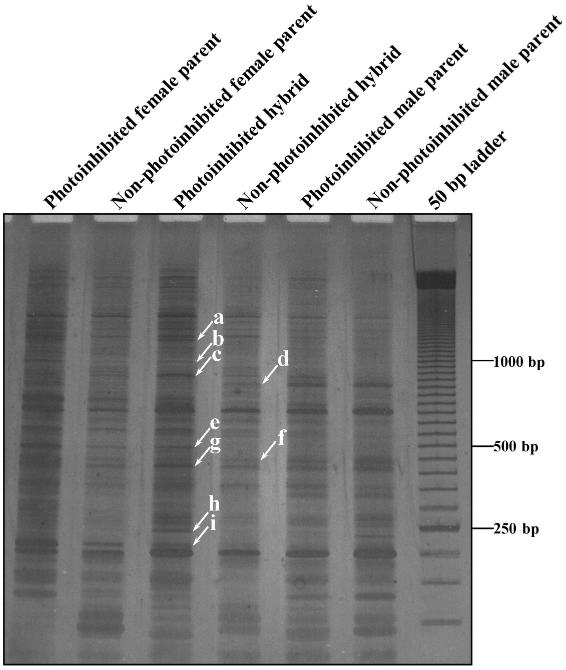

Fig. 1. An example of the electrophoretic pattern of mRNA differential display visualized by silver staining. *Arrows and the letters* "a" to "i" indicate differentially expressed cDNA fragments. The anchor primer and the arbitrary primer were HT$_{11}$G and HAP30, respectively.

Discussion

The sequence similarity analysis of the G29×280 clone suggested that it encodes a putative pre-mRNA splicing factor ATP-dependent RNA helicase in *O. sativa* ssp. *indica*. RNA helicases are ubiquitous and predicted as modulators of RNA structures with potential roles in many aspects of gene expression, including transcription, nuclear and mitochondrial RNA splicing, ribosome synthesis, translation, RNA editing, mRNA export, and mRNA turnover (Luking *et al.* 1998, de la Cruz *et al.* 1999). These proteins can be grouped into several families according to the sequences of the seven motifs. And the "DEAH-box" family is named after its invariable amino acid sequence D-E-A-H in motif II (Company *et a*l. 1991, Arenas and Abelson 1997). Four previously characterized DEAH-box proteins (PRP2, PRP16, PRP22, and PRP43) functioned in pre-mRNA splicing (Staley and Guthrie 1998). Further studies are necessary to address the question whether the G29×280 gene encodes a pre-mRNA splicing factor ATP-dependent RNA helicase in the hybrid and its possible protective functions under HI stress.

The A31×380 clone could encode a putative phosphatidylinositol 4-kinase (PI-4-K) in the hybrid Liangyoupeijiu according to the result of similarity analysis. Phosphatidylinositol (PI) is an important component of the membrane in plant cell, and its metabolizability plays important roles in signal transduction. PI-4-K catalyzes the phosphorylation of PI in the D-4 position of the inositol ring and this is the committed step in the synthetic pathway leading to phosphatidylinositol 4,5-bisphosphate (PI-4,5-P$_2$), which is then hydrolyzed by phospholipase C (PLC) into the second messenger inositol-1,4,5-trisphosphate (IP3) and diacylglycerol (DAG) (for reviews see Drøbak 1992, Gehrmann and Heilmeyer 1998). Phosphoinositides have been implicated in a number of environmental stress signalling processes, including responses to acid and osmotic stress, HI stress, and pathogen attack, as well as in regulating turgor and leaf and flower movements (Drøbak 1992, Munnik *et al.* 1998). So the A31×380 was differentially expressed and could be involved in the response to HI stress.

The G25×320 clone was identical to a cytosolic monodehydroascorbate reductase (MDAR). As stated above, the scavenging systems for ROS and the thermal dissipation depending on the xanthophyll cycle and the water-water cycle are important photo-protective mechanisms. Ascorbate is involved in regenerating Z in the xanthophyll cycle and it is efficient quencher of ROS such as superoxide radical (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radical (HO·), and singlet oxygen ($^1O_2$) (Bodannes and Chan 1979, Conklin *et al.* 1996). Obviously it plays a central role in both processes. However, all these functions depend on the continuous regeneration of ascorbate. The key function of MDAR is to reduce monodehydroascorbate to ascorbate to ensure the sustainable use of ascorbate in the cycles (Bielski 1982). The present study suggested that the MDAR was up-regulated by HI and might be involved in maintaining a larger content of ascorbate to ensure the operation of the thermal dissipation depending on the xanthophyll cycle and ROS-scavenging systems.

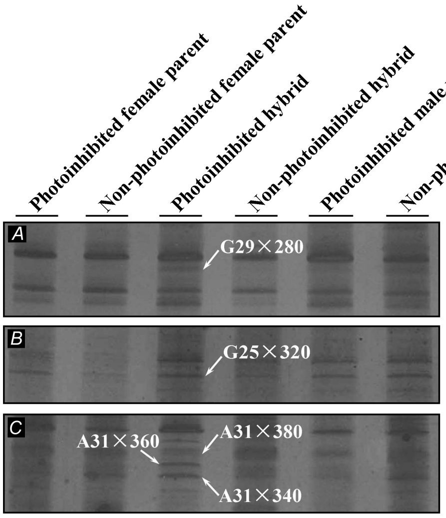

Fig. 2. Electrophoretic patterns of mRNA differential display visualized by silver staining. *Arrows* indicate 5 up-regulated cDNA fragments G29×280, A31×380, G25×320, A31×340, and A31×360. The anchor primer and the arbitrary primer were (*A*) HT$_{11}$G and HAP29, (*B*) HT$_{11}$G and HAP25, and (*C*) HT$_{11}$A and HAP31, respectively.

According to the similarity analysis, the clones of A31×340 and A31×360 might encode an ammonium transport protein (cysQ) and a DNA gyrase in some bacteria, respectively. But there are no highly similar homology sequences in rice or plant database possibly because of too short sequences of the fragments. So we have to do much work to confirm and understand their roles in responding to HI stress.

Of the 167 differentially expressed cDNA fragments, 127 (76.05 %) of them had obvious genetic origins, suggesting that most differentially expressed genes in the hybrid rice were inherited from parents. These differentially expressed cDNA fragments derived from the female parent, the male parent, and from both of them represented 15.57, 19.76, and 40.72 %, respectively. The results support the opinion that the photoinhibitory traits of F1 hybrid were controlled by the interaction of the plastid genes derived from female parent and the nuclear genes derived from male parent (Jiao and Ji 2001). The results also suggest that a great number of differentially expressed genes were inherited from both parents rather than either of them. On the other hand, some differentially expressed cDNA fragments (23.95 %) having no distinct genetic origins indicated the involvement of some unclear mechanisms in the inheritance processes from the parents to the hybrid.

cDNA Southern blot analyses (Fig. 3) confirmed the gene expression pattern of the 5 clones identified from differential display experiments, supporting that the silver-staining mRNA differential display was an effective method for characterizing genes differentially expressed under HI stress. Since its invention in 1992 (Liang and Pardee 1992), the differential display has quickly overtaken differential screening and subtractive hybridization to become the method of choice for cloning differentially expressed genes. This is due to its fairly simple equipment and technology, a thimbleful of sample, high sensitivity, and convenience of analyzing low abundant mRNA, despite of all disadvantages of this technique such as false positives and relatively short fragments (Li *et al*. 1994, Zegzouti *et al*. 1997). As an alternative, cDNA micro-array is getting more attention for its automated and high-throughput property. However, the requisitions for special equipments, exorbitant expenditure, and expensive and time-consuming process of the construction of cDNA library have limited its application.

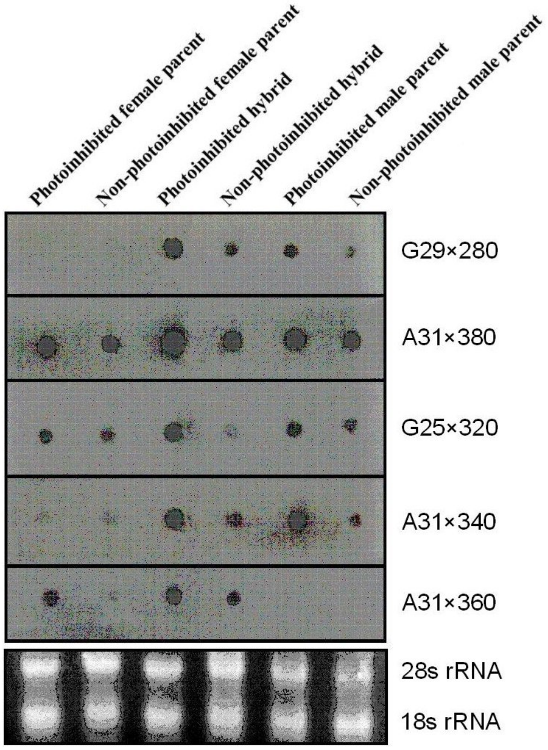

Fig. 3. cDNA Southern blot patterns of G29×280, A31×380, G25×320, A31×340, and A31×360 clones. 20 ng of cDNAs reverse transcribed from RNA samples isolated from the photoinhibited and non-photoinhibited samples from female parent, hybrid, and male parent were denatured before printed onto N$^+$ nylon membrane. The blot was probed with the differentially expressed fragments of G29×280, A31×380, G25×320, A31×340, and A31×360, and the membranes were exposed for 1–6 h.

In this study, we obtained 167 differentially expressed cDNA fragments under HI stress in the hybrid and searched for their genetic origins. In order to get more information about the differentially expressed cDNA fragments, we need to amplify their complete sequences by 5'-RACE or other techniques and perform quantitative or semi-quantitative RT-PCR or Northern blots on them to validate their changes in expression level under HI stress. As for the biological significance and physiological roles of these genes under photoinhibition, we still need to do much further work.

Reference

Altschul, S.F., Madden, T.L., Schaffer, A.A., Zhang, J., Zhang, Z., Miller, W., Lipman, D.J.: Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. – Nucl. Acids Res. **25**: 3389-3402, 1997.

Arenas, J.E., Abelson, J.N.: Prp43: an RNA helicase-like factor involved in spliceosome disassembly. – Proc. nat. Acad. Sci. USA **94**: 11798-11802, 1997.

Asada, K.: The water-water cycle in chloroplasts: Scavenging of active oxygens and dissipation of excess photons. – Annu. Rev. Plant Physiol. Plant mol. Biol. **50**: 601-639, 1999.

Bielski, B.H.J.: Chemistry of ascorbic acid radicals. – In: Seib, P.A., Tolbert, B.M. (ed.): Ascorbic Acid, Chemistry, Metabolism and Uses. Pp. 81-100. American Chemical Society, Washington 1982.

Bodannes, R.S., Chan, P.C.: Ascorbic acid as a scavenger of singlet oxygen. – FEBS Lett. **105**: 195-196, 1979.

Bohnert, H.J., Sheveleva, E.: Plant stress adaptations – making metabolism move. – Curr. Opin. Plant Biol. **1**: 267-274, 1998.

Chen, H.C., Klein, A., Xiang, M., Backhaus, R.A., Kuntz, M.: Drought- and wound-induced expression in leaves of a gene encoding a chromoplast carotenoid-associated protein. – Plant J. **14**: 317-326, 1998.

Chomczynski, P., Sacchi, N.: Single-step method of RNA isolation by acid guanidinium thiocyanate-phenol-chloroform extraction. – Anal. Biochem. **162**: 156-159, 1987.

Company, M., Arenas, J., Abelson, J.: Requirement of the RNA helicase-like protein PRP22 for release of messenger RNA from spliceosomes. – Nature **349**: 487-493, 1991.

Conklin, P.L., Williams, E.H., Last, R.L.: Environmental stress sensitivity of an ascorbic acid-deficient *Arabidopsis* mutant. – Proc. nat. Acad. Sci. USA **93**: 9970-9974, 1996.

de la Cruz, J., Kressler, D., Linder, P.: Unwinding RNA in *Saccharomyces cerevisiae*: DEAD-box proteins and related families. – Trends biochem. Sci. **24**: 192-198, 1999.

Demmig-Adams, B., Adams, W.W., III: The role of xanthophyll cycle carotenoids in the protection of photosynthesis. – Trends Plant Sci. **1**: 21-26, 1996.

Deng, X., Hu, Z.A., Wang, H.X.: mRNA differential display visualized by silver staining tested on gene expression in resurrection plant *Boea hygrometrica*. – Plant mol. Biol. Rep. **17**: 1-7, 1999.

Drøbak, B.K.: The plant phosphoinositide system. – Biochem. J. **288**: 697-712, 1992.

Dunaeva, M., Adamska, I.: Identification of genes expressed in response to light stress in leaves of *Arabidopsis thaliana* using RNA differential display. – Eur. J. Biochem. **268**: 5521-5529, 2001.

Gehrmann, T., Heilmeyer, L.M., Jr.: Phosphatidylinositol 4-kinases. – Eur. J. Biochem. **253**: 357-370, 1998.

Horton, P., Ruban, A.V.: Regulation of Photosystem II. – Photosynth. Res. **34**: 375-385, 1992.

Jagendorf, A.T.: Photophosphorylation and the Hill reaction. – Nature **191**: 679-680, 1961.

Jiao, D.M., Ji, B.H.: Photoinhibition in *indica* and *japonica* subspecies of rice (*Oryza sativa*) and their reciprocal F_1 hybrids. – Aust. J. Plant Physiol. **28**: 299-306, 2001.

Kok, B.: On the inhibition of photosynthesis by intense light. – Biochim. biophys. Acta **21**: 233-244, 1956.

Li, F.S., Barnathan, E., Kariko, K.: Rapid method for screening and cloning of cDNA generated in differential mRNA display: application of Northern blot for affinity capturing of cDNA. – Nucl. Acids Res. **22**: 1764-1765, 1994.

Liang, P., Pardee, A.B.: Differential display of eukaryotic messenger RNA by means of the polymerase chain reaction. – Science **257**: 967-971, 1992.

Long, S.P., Humphries, S., Falkowski, P.G.: Photoinhibition of photosynthesis in nature. – Annu. Rev. Plant Physiol. Plant mol. Biol. **45**: 633-662, 1994.

Luking, A., Stahl, U., Schmidt, U.: The protein family of RNA helicases. – Crit. Rev. Biochem. mol. Biol. **33**: 259-296, 1998.

Michael, J.F., Louise, B., Kevin, O., Stanislaw, K., Philip, M.M., Neil, R.B.: Control of ascorbate peroxidase 2 expression by hydrogen peroxide and leaf water status during excess light stress reveals a functional organisation of *Arabidopsis* leaves. – Plant J. **33**: 691-705, 2003.

Munnik, T., Irvine, R.F., Musgrave, A.: Phospholipid signaling in plants. – Biochim. biophys. Acta **1389**: 222-272, 1998.

Niyogi, K.K.: Photoprotection revised: Genetic and molecular approaches. – Annu. Rev. Plant Physiol. Plant mol. Biol. **50**: 333-359, 1999.

Noam, A., Hagit, Z., Susana, S., Itzhak, O.: Photoinhibition – a historical perspective. – Photosynth. Res. **76**: 343-370, 2003.

Pfündel, E., Bilger, W.: Regulation and possible function of the violaxanthin cycle. – Photosynth. Res. **42**: 89-109, 1994.

Powles, S.B.: Photoinhibition of photosynthesis induced by visible light. – Annu. Rev. Plant Physiol. **35**: 15-44, 1984.

Staley, J., Guthrie, C.: Mechanical gadgets in the spliceosome: clocks, motors, springs and things. – Cell **92**: 315-326, 1998.

Wang, Q., Zhang, Q.D., Zhu, X.G., Lu, C.M., Kuang, T.Y., Li, C.Q.: PSII photochemistry and xanthophylls cycle in two superhigh-yield rice hybrids, Liangyoupeijiu and Hua-an 3 during photoinhibition and subsequent restoration. – Acta bot. sin. **44**: 1297-1302, 2002.

Whitmarsh, J., Samson, G., Poulson, M.: Photoprotection in photosystem II - the role of cytochrome *b*559. – In: Baker, N.R., Bowyer, J.R. (ed.): Photoinhibition of Photosynthesis From Molecular Mechanism to the Field. Pp. 75-93. Bios Scientific Publishers, Oxford 1994.

Zegzouti, H., Marty, C., Jones, B., Bouquin, T., Latché, A., Pech, J.C., Bouzayen, M.: Improved screening of cDNAs generated by mRNA differential display enables the selection of true positives and the isolation of weekly expressed messages. – Plant mol. Biol. Rep. **15**: 236-245, 1997.