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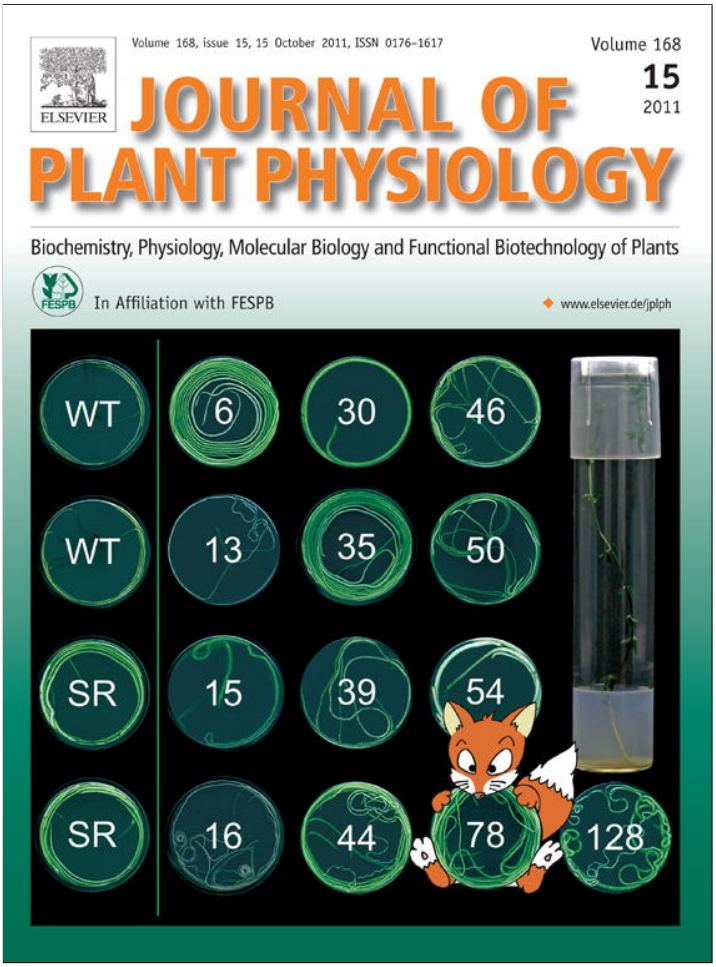

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A chloroplast-targeted DnaJ protein AtJ8 is negatively regulated by light and has rapid turnover in darkness

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ABSTRACT

The DnaJ proteins (also called as J proteins, J domain proteins or HSP40 proteins) function as molecular co-chaperones for the HSP70 proteins. We assessed the expression of the small chloroplast-targeted DnaJ protein, the AtJ8 protein, by subjecting the wild type *Arabidopsis* plants to different illumination conditions. It is shown that the expression of the transcripts and proteins of the *ATJ8* gene is primarily regulated at the level of transcription. When plants were incubated under high light for 3 h, both the transcripts and proteins were completely abolished. Upon transfer of plants to darkness, the transcripts started rapidly accumulating, and subsequently, the AtJ8 protein became visible after 2 h in darkness. Conversely, incubation of plants in darkness or under low light intensities induced expression of the *ATJ8* transcripts and proteins. Feeding plants with sugars clearly decreased the transcript and protein levels, and incubation with cycloheximide revealed a rapid turnover for AtJ8 in darkness. Moreover, the AtJ8 protein was found to be nearly missing from the *var1* mutant, which lacks the FTSH5 protease. It is concluded that AtJ8 is expressed mainly in darkness, is prone to a rapid turnover but is partially stabilized by the FTSH proteases.

Introduction

During the past ten years, genomics and proteomics analyses have revealed the presence of a number of regulatory auxiliary proteins in chloroplasts (Mulo et al., 2008). In variance to structural proteins, the nuclear-encoded, chloroplast targeted regulatory proteins such as chaperones, kinases, phosphatases and proteases are typically present in low, sub-stoichiometric amounts, and are often expressed only transiently under a specific developmental or physiological phase or under certain environmental condition. As these proteins assist in the biogenesis, maintenance and stability of the thylakoid membrane complexes, and regulate the photosynthetic reactions according to environmental cues, they are crucial for the efficient function of the photosynthetic machinery.

Chaperones assist other proteins in various cellular functions, e.g. by aiding the newly synthesized proteins to fold correctly, or by preventing protein aggregation. The DnaJ proteins (also referred to as J proteins, J domain proteins or HSP40 proteins) function as molecular co-chaperones of the HSP70 proteins (Kampinga and Craig, 2010; Rajan and D'Silva, 2009). During the past few years, the knowledge concerning the DnaJ proteins in chloroplasts has gradually increased and it now seems likely that numerous DnaJ proteins participate in fundamental processes of chloroplast differentiation and function. For instance, in green algae *Chlamydomonas reinhardtii*, five DnaJ proteins (CDJ1-5) have been characterized thus far (Liu et al., 2005, 2007; Willmund et al., 2008; Dorn et al., 2010; Heide et al., 2009), and of these, CDJ2 functions in thylakoid membrane biogenesis together with the vesicle inducing protein VIPP1 (Liu et al., 2005, 2007). In *Arabidopsis*, ARC6 (ACCUMULATION AND REPLICATION OF CHLOROPLASTS 6) has been localized to the chloroplast envelope membrane, where it participates in the division of plastids (Vitha et al., 2003). Moreover, CYO1 (COTYLEDON-SPECIFIC CHLOROPLAST BIOGENESIS FACTOR) resides in thylakoid membranes and functions in chloroplast differentiation (Shimada et al., 2007), whereas OWL1 (ORIENTATION UNDER VERY LOW FLUENCES OF LIGHT1) is a J-domain protein important for the early growth under low light conditions (Kneissl et al., 2009).

We recently addressed the functional role of three small chloroplast-targeted DnaJ proteins AtJ8 (AT1G80920), AtJ11 (AT4G36040) and AtJ20 (AT4G13830), by using *Arabidopsis* knock-

Abbreviation: WT, wild type.

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out mutants (Chen et al., 2010). It was shown that the lack of any one of these proteins caused multiple deleterious effects on photosynthesis, for instance, the photosynthetic efficiency of the knockouts was diminished and the PSII complexes were destabilized. Moreover, the global analyses of gene expression revealed that the knockouts over-express genes encoding stress-related transcription factors and enzymes, which detoxify reactive oxygen species. As a consequence, the *atj8*, *atj11* and *atj20* mutants showed higher tolerance against oxidative stress as compared to the wild-type plants (Chen et al., 2010).

In the present work, we investigated the expression of AtJ8 in more detail to get insights into the light-dark regulation of this small DnaJ protein. We show that the expression of the transcripts and proteins of the *ATJ8* gene is primarily regulated at the level of transcription, being inhibited in light by photosynthesis-related signals. The AtJ8 protein is expressed mainly in darkness, is prone to a rapid turnover but is partially stabilized by the FTSH proteases.

Materials and methods

Plant material and treatments

Arabidopsis thaliana ecotype Columbia (Col-0) wild-type (WT) and homozygous T-DNA insertion mutant lines *atj8*, deficient of the AtJ8 (AT1G80920) protein (Chen et al., 2010), *var1-1* and *var2-2*, deficient of the FTSH5 and FTSH2 proteins, respectively (Sakamoto et al., 2002), were used in the experiments. Plants were grown at 23 °C under a photon flux density of 150 μmol photons m^{-2} s^{-1} under 8 h/16 h light/dark rhythm, unless otherwise stated. Five to six week old leaves were used in experiments. In order to feed substances through the petiole, 6–8 leaves were pooled from different plants and fed in a solution overnight in darkness, unless otherwise indicated. Used concentrations were as follows: 50 mM glucose, 50 mM sucrose, 50 mM fructose, and 50 μM cycloheximide.

For the biomass experiments, the used light intensities and rhythms were as follows: growth light: 150 μmol photons m^{-2} s^{-1} under 8 h/16 h light/dark; low light: 40 μmol photons m^{-2} s^{-1}, 8 h/16 h light/dark; high light: 600 μmol photons m^{-2} s^{-1}, 8 h/16 h light/dark; long-day growth light: 120 μmol photons m^{-2} s^{-1}, 16 h/8 h light/dark and continuous growth light: 120 μmol photons m^{-2} s^{-1}, 24 h light. The dry weight of the WT and *atj8* plants was measured after drying the plant rosettes in oven (60 °C) for two days. The data was analysed with the PASW Statistics tool package (version 18).

RNA and protein analyses

Total cellular RNA and proteins were extracted from the same samples using the Trizol reagent (Invitrogen, Carlsbad, CA, USA) according to the manufacturer's protocol. RNA blotting was performed as described previously (Piippo et al., 2006). Protein contents were determined using a detergent-compatible protein assay kit (Bio-Rad, Hercules, CA). Proteins were separated by SDS-PAGE using 15% (w/v) acrylamide gels with 6 M urea (Laemmli, 1970). After electrophoresis, the proteins were electroblotted to a polyvinylidene fluoride membrane (Millipore, Billerica, MA), blocked with 5% milk (BioRad Hercules, CA, USA), probed with the AtJ8 antibody (Chen et al., 2010) and detected by the enhanced chemiluminesence detection method.

Results

To clarify the light-dark regulation of the *ATJ8* gene, WT *Arabidopsis* plants were first treated in high light (500 μmol photons m^{-2} s^{-1}). As shown in Fig. 1A, the 3 h illumination of plants in high light completely abolished the *ATJ8* transcripts and the AtJ8 proteins from the leaves (Fig. 1A, time point 0). Upon subsequent transfer of plants to darkness, the transcripts started accumulating already within 30 min, and AtJ8 proteins became visible by immunoblotting after 2 h in darkness (Fig. 1A). Conversely, overnight incubation of plants in darkness induced high levels of *ATJ8* transcripts and proteins (Fig. 1B), but already in 30 min after the onset of the light period the transcript levels had decreased to less than a half. Protein levels followed the transcript levels and were markedly reduced after 1 h of light treatment.

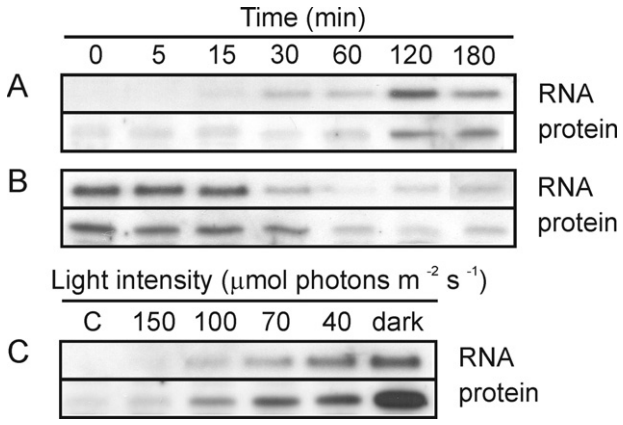

Fig. 1. Alterations in the *ATJ8* gene expression in WT *Arabidopsis* plants at transcript and protein level. Total cellular RNA and proteins were extracted from the same samples, followed by RNA blotting with the *ATJ8* probe or immunodetection with the AtJ8 antibody. 5 μg of RNA and 30 μg of protein were loaded. (A) The plants were treated with high light (500 μmol photons m^{-2} s^{-1}) for 3 h (time point 0), and subsequently transferred to darkness. (B) The *Arabidopsis* WT plants were incubated under darkness for 18 h (time point 0), and transferred to growth light (150 μmol photons m^{-2} s^{-1}). (C) The plants were transferred from growth light (C) (150 μmol photons m^{-2} s^{-1}) to the indicated light intensities for 3 h.

Next we tested whether the induction of *ATJ8* transcripts and proteins requires complete darkness, or whether it is a light-intensity dependent phenomenon. The plants were subjected to different light intensities (150, 100, 70, and 40 μmol photons m^{-2} s^{-1} and darkness) for 3 h. Both the transcript and protein levels were very low after the 3 h treatment in 150 μmol photons m^{-2} s^{-1} (Fig. 1C). Additional treatment of 3 h in 150 μmol photons m^{-2} s^{-1} did not further change the transcript levels. Noteworthy, the lower the fluence rate was upon 3 h illumination of plants, the higher were the mRNA and protein amounts, and the highest levels of both the mRNA and protein were recorded in complete darkness (Fig. 1C).

In order to test whether the AtJ8 protein is synthesized in darkness but degraded only in the light, or whether degradation occurs also in darkness, the protein synthesis inhibitor cycloheximide was fed to plants in darkness through the petiole. The plants were first let to synthesize the protein overnight in darkness, then cycloheximide was added and the leaves were further incubated in darkness for 1, 2, 3 and 6 h. Only 1 h incubation with cycloheximide in darkness already clearly decreased the content of the AtJ8 protein as compared to plants fed only with water (Fig. 2). Furthermore, whereas the AtJ8 protein amount remained constant in leaves incubated in water, in plants fed with cycloheximide the AtJ8 protein amount gradually decreased during the subsequent hours, being completely vanished after 6 h in darkness. This provides evidence that in addition to the rapid synthesis in darkness, the AtJ8 protein is also constantly degraded in darkness, thus exhibiting a relatively rapid turnover. Notably, the *ATJ8* mRNA levels remained unchanged, or were even somewhat increased, upon decrease in the AtJ8 protein amounts in the presence of cycloheximide (Fig. 2),

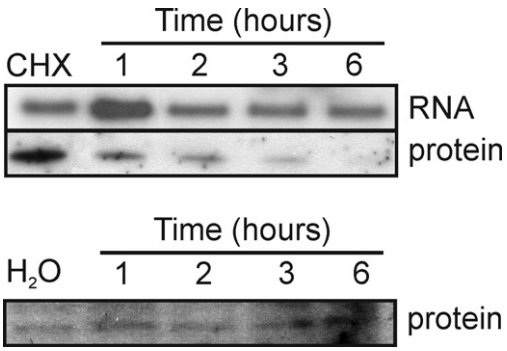

Fig. 2. Effect of protein synthesis inhibitor cycloheximide on the *ATJ8* transcript and protein amounts. WT leaves were incubated in water overnight to induce AtJ8 synthesis, after which either cycloheximide (CHX) or water (H_2O) was added and incubation was continued in darkness during indicated hours. Total cellular RNA and proteins were extracted, followed by RNA blotting with the *ATJ8* probe and immunodetection with the AtJ8 antibody, respectively. 7 μg of RNA and 30 μg of protein were loaded.

indicating that the protein itself did not control the transcription of the *ATJ8* gene.

Nearly linear response of the *ATJ8* transcript and protein accumulation to decreasing light intensity (Fig. 1C) suggests the involvement of photosynthetic redox reactions or end products, such as sugars, as mediators of the signals to decrease *ATJ8* transcription in light. We tested this hypothesis by feeding plants with different sugars through the petiole. Indeed, feeding sucrose, glucose or fructose overnight in darkness clearly decreased the transcript and protein levels as compared to control leaves with petioles incubated in water (Fig. 3).

Rapid degradation of the AtJ8 protein both in light and darkness raises the question about proteases involved. Of several families of chloroplast proteases, the FTSH proteases are involved in the repair cycle of PSII (Lindahl et al., 2000) and have a direct role in the function of photosynthesis. Two mutants deficient of the FTSH5 and FTSH2 proteins (*var1* and *var2*, respectively) are the best characterized FTSH protease mutants (Sakamoto et al., 2002; Zaltsman et al., 2005). To test whether FTSH2 and/or FTSH5 are involved in *ATJ8* expression, the *var1* and *var2* mutant plants were analysed for their *ATJ8* gene and protein expression. The plants were exposed to growth light for 6 h, or to growth light for 3 h followed by 3 h in darkness. The *ATJ8* mRNA was expressed both in *var1* and *var2* in darkness but was absent in light, similar to the wild type plants (Fig. 4). Although the *ATJ8* transcript level was similar or even slightly higher in the *var1* and *var2* mutants under darkness as compared to WT, it was interesting to note that the amount of the AtJ8 protein was lower in the *var2* mutants than in WT under darkness, and was nearly missing from the *var1* mutant

Finally, in order to test whether the negative correlation between light and the *ATJ8* expression results in visual phenotype,

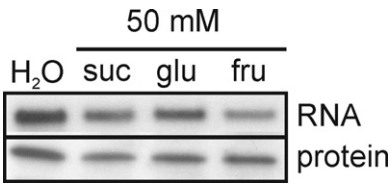

Fig. 3. Decrease in the *ATJ8* transcript and protein amounts due to sugar feeding. Petiols of the WT leaves were incubated overnight in darkness in water (H_2O) or in 50 mM sucrose (suc), glucose (glu) or fructose (fru). Total cellular RNA and proteins were extracted from the same samples, followed by RNA blotting with the *ATJ8* probe or immunodetection with the AtJ8 antibody. 5 μg of RNA and 30 μg of protein were loaded.

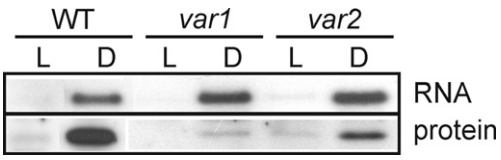

Fig. 4. Comparison of the ATJ8 transcript and protein amounts in WT, *var1* and *var2* plants after 6 h in growth light (150 μmol photons m^{-2} s^{-1}) (L) or after 3 h in growth light followed by 3 h in darkness (D). Total cellular RNA and proteins were extracted from the same samples, followed by RNA blotting with the *ATJ8* probe or immunodetection with the AtJ8 protein. 5 μg of RNA or 30 μg of protein were loaded.

WT and the *atj8* mutant plants were grown under various light environments and the biomass of the plants was measured (data not shown). Neither the genotype (WT versus the *atj8* mutant) nor the light conditions were associated with rosette biomasses' (ANOVA, genotype $F_{1.183} = 0.220$, $p = 0.639$; light condition $F_{1.183} = 0.140$, $p = 0.709$; interaction term: genotype × light condition $p = 0.552$).

Discussion

Transcription of the nucleus-located *ATJ8* gene, encoding a small chloroplast-targeted DnaJ protein AtJ8, was previously found to be strongly induced in darkness (Piippo et al., 2006). Furthermore, the biochemical characterization of the *atj8* knock-out mutants suggested that AtJ8 is possibly involved in stabilization of the Rubisco and the Rubisco activase proteins, as both the enzyme amounts and the capacity of CO_2 assimilation were lowered in the *atj8* mutant (Chen et al., 2010). In the present study we addressed the regulation of AtJ8 in more detail by exposing the WT plants to different light conditions, followed by the *ATJ8* mRNA and protein analyses.

First of all, we note that the primary regulatory switch in *ATJ8* expression is likely to be at the transcription level, since the shifts of plants to different light intensities or feeding them with sugars induced similar responses both at the transcript and protein levels (Figs. 1 and 3). The shift of plants from high light to darkness resulted in accumulation of both the *ATJ8* mRNA and the AtJ8 protein (Fig. 1A). It was further revealed that not only darkness, but also a decrease in light intensity gradually induced mRNA and protein accumulation (Fig. 1C). Moreover, both the *ATJ8* transcript and protein amounts started decreasing when dark-adapted plants were shifted to growth light (Fig. 1B). The response in transcript level was detectable already after 30 min of dark or light incubation (Fig. 1A and B), indicating a fairly rapid response. Relatively quick transcriptional response upon shift to darkness was also revealed from an extensive microarray study of the early dark response, in which down-regulation of several genes occurred only after 1 h of darkness (Kim and von Arnim, 2006). Changes in the AtJ8 protein levels generally lagged behind the mRNA levels by half an hour (Fig. 1A and B), implying the induction of translation as soon as the mRNAs starts to accumulate.

Since photosynthesis is driven by light, most of research in the field has focused on light-induced reactions and the expression and function of chloroplast proteins in darkness have gained less attention. Although both the photosynthetic electron transfer and carbon fixation are inhibited in darkness, there are several other cellular processes particularly active in darkness. For instance, starch and sugars are being decomposed, extensive abscisic acid signalling is induced and mainly because of mitochondrial respiration, there is also a production of reactive oxygen species (Kim and von Arnim, 2006; Affourtit et al., 2001; Bechtold et al., 2004). Based on our results, the response of both the *ATJ8* transcripts and the AtJ8 proteins to changes in light intensity was rapid (Fig. 1), as was also the turnover of AtJ8 with half-life less than one hour in

darkness (Fig. 2). It is evident that AtJ8 functions mainly in darkness and participates in transient and dynamic dark-regulation of chloroplast metabolism. This is most likely related to the role of the AtJ8 protein as a chaperone. Recently, a chaperone function in darkness was suggested for a Tic62 protein (Benz et al., 2009), which was shown to form a complex with the chloroplast ferredoxin NADP(H) oxidoreductase (FNR) under darkness, and after illumination the complex was shown to dissociate (Benz et al., 2009, 2010). It was postulated that Tic62 protects FNR against degradation in darkness, when FNR is not needed for photosynthesis (Benz et al., 2009, 2010; Mulo, 2010). Reduced content of Rubisco and Rubisco activase in the *atj8* mutant (Chen et al., 2010) may indicate similar type of function for the AtJ8 protein, although direct interaction with Rubisco and/or Rubisco activase could not be demonstrated.

Externally added sucrose, glucose and fructose clearly reduced both the *ATJ8* transcript and protein levels (Fig. 3) indicating that the chloroplast metabolic state, rather than light *per se*, initially regulates AtJ8 (Piippo et al., 2006). Similar to *ATJ8*, adding of external sugars was shown to repress the expression of several dark-induced genes (Fujiki et al., 2001). Furthermore, short-term dark treatment has been shown to affect the expression of several genes related to sugar metabolism and starvation (Kim and von Arnim, 2006). Clear down-regulation of the *ATJ8* gene by sugars also supports our previous finding that in *Arabidopsis* gene expression profiles, there is a correlation between the sugar levels and extended night (Piippo et al., 2006).

Accumulation of the ATJ8 protein in darkness was strongly diminished in the absence of the FTSH5 protease and somewhat less stringently also in the absence of the FTSH2 protein (Fig. 4). Thus, it seems that the FTSH protease rather stabilizes the AtJ8 protein in chloroplasts in darkness than degrades it. A simple functional scenario could be that the AtJ8 protein associates with the FTSH protease in darkness and thus prevents the degradation of FTSH target proteins in darkness. Fast degradation of the AtJ8 proteins upon turning the lights on might then release the FTSH proteases to function in the biogenesis and repair of chloroplast protein complexes, the processes that are known to require light. It is also conceivable that the putative FTSH–AtJ8 complex associates with yet another target molecule (e.g. Rubisco and/or Rubisco activase) in darkness. Such hypothetical complex could function to prevent the aggregation and irreversible inhibition of the target proteins which are needed only in light. Both of these putative functions of the AtJ8 protein can explain the reduction of Rubisco and Rubisco activase observed in the *atj8* mutants as compared to WT (Chen et al., 2010).

Finally we tested whether there are differences in biomass production between the *atj8* mutants and WT plants grown under various light-dark conditions. The *atj8* mutants showed no difference in their biomass as compared to the WT plants in any of the light conditions studied. The equal size of the *atj8* plants could be due to compensatory mechanisms, as the lack of AtJ8 is perhaps replaced by other DnaJ proteins. When searching for genes that are co-regulated with *ATJ8* by using the ATTED-II database (Obayashi et al., 2007) or the CressExpress tool (Srinivasasainagendra et al., 2008), all the three small chloroplast-targeted J-domain proteins AtJ8, AtJ11 (AT4G36040), and AtJ20 (AT4G13830) (Chen et al., 2010) demonstrate a rather similar expression profile and possibly AtJ11, AtJ20 and AtJ8 are at least partially redundant in their function.

To conclude, we have shown that AtJ8, a small chloroplast-targeted DnaJ protein, is tightly regulated by chloroplast signals, being down-regulated by increasing light intensities. Sugars are able to partially repress the expression of AtJ8 in darkness. Moreover, the AtJ8 protein is subject to rapid turnover but is partially stabilized by the FTSH proteases. Thus, AtJ8 seems to have a transient function in cellular homeostasis. It is apparently needed only in darkness but strong accumulation of the protein would have harmful effects and this is prevented by a rapid turnover of AtJ8.

Acknowledgments

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References

Affourtit C, Krab K, Moore AL. Control of plant mitochondrial respiration. Biochim Biophys Acta 2001;1504:58–69.
Bechtold U, Murphy DJ, Mullineaux PM. Arabidopsis peptide methionine sulfoxide reductase2 prevents cellular oxidative damage in long nights. Plant Cell 2004;16:908–19.
Benz JP, Lintala M, Soll J, Mulo P, Bolter B. A new concept for ferredoxin–NADP(H) oxidoreductase binding to plant thylakoids. Trends Plant Sci 2010;15:608–13.
Benz JP, Stengel A, Lintala M, Lee YH, Weber A, Philippar K, et al. Arabidopsis Tic62 and ferredoxin–NADP(H) oxidoreductase form light-regulated complexes that are integrated into the chloroplast redox poise. Plant Cell 2009;21:3965–83.
Chen KM, Holmstrom M, Raksajit W, Suorsa M, Piippo M, Aro EM. Small chloroplast-targeted DnaJ proteins are involved in optimization of photosynthetic reactions in *Arabidopsis thaliana*. BMC Plant Biol 2010;10:43.
Dorn KV, Willmund F, Schwarz C, Henselmann C, Pohl T, Hess B, et al. Chloroplast DnaJ-like proteins 3 and 4 (CDJ3/4) from *Chlamydomonas reinhardtii* contain redox-active Fe–S clusters and interact with stromal HSP70B. Biochem J 2010;427:205–15.
Fujiki Y, Yoshikawa Y, Sato T, Inada N, Ito M, Nishida I, et al. Dark-inducible genes from *Arabidopsis thaliana* are associated with leaf senescence and repressed by sugars. Physiol Plant 2001;111:345–52.
Heide H, Nordhues A, Drepper F, Nick S, Schulz-Raffelt M, Haehnel W, et al. Application of quantitative immunoprecipitation combined with knockdown and cross-linking to Chlamydomonas reveals the presence of vesicle-inducing protein in plastids 1 in a common complex with chloroplast HSP90C. Proteomics 2009;9:3079–89.
Kampinga HH, Craig EA. The HSP70 chaperone machinery: J proteins as drivers of functional specificity. Nat Rev Mol Cell Biol 2010;11:579–92.
Kim BH, von Arnim AG. The early dark-response in *Arabidopsis thaliana* revealed by cDNA microarray analysis. Plant Mol Biol 2006;60:321–42.
Kneissl J, Wachtler V, Chua NH, Bolle C. OWL1: an Arabidopsis J-domain protein involved in perception of very low light fluences. Plant Cell 2009;21:3212–25.
Laemmli UK. Cleavage of structural proteins during the assembly of the head of bacteriophage T4. Nature 1970;227:680–5.
Lindahl M, Spetea C, Hundal T, Oppenheim AB, Adam Z, Andersson B. The thylakoid FtsH protease plays a role in the light-induced turnover of the photosystem II D1 protein. Plant Cell 2000;12:419–31.
Liu C, Willmund F, Golecki JR, Cacace S, Hess B, Markert C, et al. The chloroplast HSP70B-CDJ2-CGE1 chaperones catalyse assembly and disassembly of VIPP1 oligomers in Chlamydomonas. Plant J 2007;50:265–77.
Liu C, Willmund F, Whitelegge JP, Hawat S, Knapp B, Lodha M, et al. J-domain protein CDJ2 and HSP70B are a plastidic chaperone pair that interacts with vesicle-inducing protein in plastids 1. Mol Biol Cell 2005;16:1165–77.
Mulo P. Chloroplast-targeted ferredoxin–NADP(+) oxidoreductase (FNR): structure, function and location. Biochim Biophys Acta 2010., doi:10.1016/j.bbabio.2010.10.001.
Mulo P, Sirpio S, Suorsa M, Aro EM. Auxiliary proteins involved in the assembly and sustenance of photosystem II. Photosynth Res 2008;98:489–501.
Obayashi T, Kinoshita K, Nakai K, Shibaoka M, Hayashi S, Saeki M, et al. ATTED-II: a database of co-expressed genes and cis elements for identifying coregulated gene groups in Arabidopsis. Nucleic Acids Res 2007;35:D863–9.
Piippo M, Allahverdiyeva Y, Paakkarinen V, Suoranta UM, Battchikova N, Aro EM. Chloroplast-mediated regulation of nuclear genes in *Arabidopsis thaliana* in the absence of light stress. Physiol Genomics 2006;25:142–52.
Rajan VB, D'Silva P. *Arabidopsis thaliana* J-class heat shock proteins: cellular stress sensors. Funct Integr Genomics 2009;9:433–46.
Sakamoto W, Tamura T, Hanba-Tomita Y, Murata M, Sodmergen. The VAR1 locus of Arabidopsis encodes a chloroplastic FtsH and is responsible for leaf variegation in the mutant alleles. Genes Cells 2002;7:769–80.
Shimada H, Mochizuki M, Ogura K, Froehlich JE, Osteryoung KW, Shirano Y, et al. Arabidopsis cotyledon-specific chloroplast biogenesis factor CYO1 is a protein disulfide isomerase. Plant Cell 2007;19:3157–69.
Srinivasasainagendra V, Page GP, Mehta T, Coulibaly I, Loraine AE. CressExpress: a tool for large-scale mining of expression data from Arabidopsis. Plant Physiol 2008;147:1004–16.
Vitha S, Froehlich JE, Koksharova O, Pyke KA, van Erp H, Osteryoung KW. ARC6 is a J-domain plastid division protein and an evolutionary descendant of the cyanobacterial cell division protein Ftn2. Plant Cell 2003;15:1918–33.
Willmund F, Dorn KV, Schulz-Raffelt M, Schroda M. The chloroplast DnaJ homolog CDJ1 of *Chlamydomonas reinhardtii* is part of a multichaperone complex containing HSP70B, CGE1, and HSP90C. Plant Physiol 2008;148:2070–82.
Zaltsman A, Ori N, Adam Z. Two types of FtsH protease subunits are required for chloroplast biogenesis and Photosystem II repair in Arabidopsis. Plant Cell 2005;17:2782–90.