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FtsH facilitates proper biosynthesis of photosystem I in *Arabidopsis thaliana*

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Abstract

Thylakoid membrane-bound FtsH proteases have a well-characterized role in degradation of photosystem (PS)II reaction center protein D1 upon repair of photodamaged PSII. Here we show that the Arabidopsis *var1* and *var2* mutants, devoid of either the FtsH5 or the FtsH2 protein, respectively, are capable of normal D1 protein turnover under moderate growth light intensity (ML). Instead, they both demonstrate a significant scarcity of PSI complexes. It is further shown that the reduced level of PSI does not result from accelerated photodamage of the PSI centers in *var1* or *var2* under ML. On the contrary, radiolabeling experiments revealed impaired synthesis of the PsaA/B reaction center proteins of PSI, which was accompanied by accumulation of PSI specific assembly factors. The *psaA/B* transcript accumulation and translation initiation, however, occurred in *var1* and *var2* mutants similarly to that in wild-type Arabidopsis, referring to problems in later stages of PsaA/B protein expression in the two *var* mutants. Presumably, the thylakoid membrane-bound FtsH5 and FtsH2 have dual functions in the maintenance of photosynthetic complexes. In addition to their function as a protease in degradation of the photodamaged D1 protein, they are also required, either directly or indirectly, for early assembly of the PSI complexes.

1. **Introduction**

Photosynthetic light reactions are driven by the thylakoid membrane-embedded multi-subunit pigment-protein complexes photosystem (PS)II and PSI (associated with their light harvesting antennas, LHCII and LHCI, respectively) and the cytochrome (Cyt) b_6f complex in cooperation with mobile electron carriers plastoquinone and plastocyanine. PSII performs highly oxidizing chemistry of water splitting, thereby inducing photo-oxidative damage to the D1 subunit of PSII (Tyystjärvi and Aro, 1996). In order to maintain the photosynthetic apparatus functional, photodamaged PSII complexes are subjected to a multistep repair cycle (Aro et al., 1993; Baena-Gonzalez and Aro, 2002; Nickelsen and Rengstl, 2013). PSII repair takes place primarily in the stroma-exposed thylakoid membranes and involves (*i*) partial disassembly of the PSII holocomplex, (*ii*) degradation of the damaged D1 protein, (*iii*) co-translational insertion of the new D1 copy to PSII, (*iv*) carboxyl terminal processing of the newly-synthetized D1 protein and (*v*) reassembly and activation of the functional PSII complex. These processes are assisted by an array of auxiliary proteins such as kinases, phosphatases, proteases and chaperones, which are located in the chloroplast stroma, thylakoid membrane and thylakoid lumen (Mulo et al., 2008; Chi et al., 2012; Suorsa et al., 2014).

PSI has generally been regarded as a robust photosystem and in plants it is protected *in vivo* by a highly efficient antioxidant network, which scavenges reactive oxygen species that otherwise would have detrimental damaging effects on the complex (Asada, 1999). Likewise, PROTON GRADIENT REGULATION5 (PGR5) protein-dependent processes and photoinhibition of PSII protect plant PSI against photodamage (Munekage et al., 2002; Shikanai, 2014; Tikkanen et al., 2014). PSI photoinhibition has been reported to take place under specific conditions, such as a combination of chilling temperature and low light intensity or under fluctuating light conditions, particularly in the absence of the PGR5 protein (Terashima et al., 1994; Sonoike et al., 1995; Tjus et al., 1998; Zhang and Scheller, 2004; Suorsa et al., 2012). The efficient repair mechanism has been considered not to exist for PSI, and thus its photoinhibition is likely to lead to a degradation of the entire PSI complex (Kudoh and Sonoike, 2002; Zhang and Scheller, 2004; Jensen et al., 2007; Sonoike, 2011), followed by *de novo* biogenesis of the complex. The PSI biosynthesis pathway is still rather poorly characterized (Schöttler et al., 2011). Even if the PSI-LHCI assembly steps remain elusive, several auxiliary proteins have been identified that transiently assist the biogenesis

and assembly of PSI (reviewed in (Schöttler et al., 2011)), and novel PSI assembly factors are constantly discovered (Liu et al., 2012; Fristedt et al., 2014; Roose et al., 2014).

FtsH proteins constitute a family of ATP-dependent membrane-bound metalloproteases found in eubacteria, animals and plants, and are known to have a crucial role in proteolysis of membrane-embedded proteins (Ito and Akiyama, 2005; Wagner et al., 2012). The Arabidopsis (*Arabidopsis thaliana*) genome encodes a total of twelve FtsH proteins. Of these, FtsH1, FtsH2, FtsH5 and FtsH8 have been shown to reside in the thylakoid membrane and to have a well-characterized role in degradation of the damaged D1 protein (Lindahl et al., 2000; Bailey et al., 2002). FtsH-mediated degradation of the D1 protein occurs in co-operation with the lumenal DegP-type serine proteases Deg1, Deg5 and Deg8 (Kapri-Pardes et al., 2007; Sun et al., 2007; Kato et al., 2012b). The homologous FtsH1 and FtsH5 proteins are referred to as type A and FtsH2 and FtsH8 as type B subunits of the FtsH complex. In its active form, the thylakoid membrane FtsH forms a ring-shaped hetero-hexameric complex, which has been reported to be composed of type A subunits and type B subunits (Yu et al., 2004; Yu et al., 2005; Zaltsman et al., 2005b; Moldavski et al., 2012). FtsH2 and FtsH5 are the major thylakoid membrane FtsH subunits, while FtsH1 and FtsH8 are less abundant (Sinvany-Villalobo et al., 2004). The amount of FtsH5 in wild type (WT) Arabidopsis plants is approximately 60% of the amount of the dominant FtsH2 protein (Sinvany-Villalobo et al., 2004). Mutants deficient in FtsH5 (*var1*) or FtsH2 (*var2*) show variegated phenotype indicating involvement of these proteins in the biogenesis (Zaltsman et al., 2005a; Kato et al., 2007) and maintenance (Kato et al., 2012a) of the thylakoid membrane. Moreover, the *var1* and *var2* mutant plants show attenuated D1 degradation under high light intensities (Lindahl et al., 2000; Sakamoto et al., 2002; Kato et al., 2009). Nevertheless, attenuated degradation of the damaged D1 protein was shown not to contribute to the leaf variegation phenotype, at least in *var2* (Kato et al., 2009).

Here, we took a more holistic approach, using the Arabidopsis mutant lines *var1* and *var2,* to elucidate the consequences of the abnormally low amount of the FtsH protease in the thylakoid membrane on the components and composition of the entire photosynthetic electron transfer chain. It is demonstrated that under moderate growth light (ML) intensities, the *var1* and *var2* mutant plants do not suffer from inefficient PSII turnover. Instead, the loss of either FtsH2 or FtsH5 leads to significantly impaired biosynthesis of PSI.

2. Results

2.1. Low amount of PSI subunits in *var1* and *var2* thylakoids under ML intensities

The role of the FtsH2 and FtsH5 proteins was addressed under ML intensities (120 µmol photons $m^{-2}s^{-1}$ in 8h light regime at 23ºC), instead of subjecting the *var1* and *var2* plants to high light intensities that induce extensive damage of the PSII centers followed by impaired D1 degradation (Lindahl et al., 2000; Sakamoto et al., 2002; Kato et al., 2009). The *var2* plants, lacking the most abundant FtsH2 subunit of the FtsH holocomplex, showed drastic growth defects as compared to WT and *var1* plants (Supplementary figure 1). To exclude the potential effect of leaf age on accumulation of thylakoid membrane protein complexes, both six-week-old and eight-week-old plants were used as experimental material. First, an immunodetection of diagnostic subunits of the major thylakoid protein complexes was performed from the WT, *var1* and *var2* plants. The gels were loaded on chlorophyll (Chl) basis to overcome normalization problems caused by the variegation phenotype.

The total amount of FtsH proteins was reduced in both *var1*, and particularly in *var2* as compared to WT, evidenced by immunoblotting with the antibody against recombinant FtsH1 that recognizes all four thylakoid-bound FtsHs (Figure 1A). This is in line with a previous report (Sinvany-Villalobo et al., 2004). The amount of PSII core protein D1 did not differ between the WT, *var1* and *var2* plants. Somewhat higher amounts of Cyt b_6f and ATP synthase, represented by Cyt *f* and Atpβ, respectively, were observed in *var1* as compared to WT. Of these, Atpβ was present in higher amounts also in *var2*, when expressed on chl basis, as compared to WT. Instead, the amount of the PSI core protein PsaB was lower in both the *var1* and *var2* mutant plants as compared to WT. Similar to PsaB, the LHCII docking proteins PsaL and PsaH (Lunde et al., 2000) showed decreased accumulation in the *var1* and *var2* plants as compared to WT (Figure 1B, C). The amounts of PsaD, PsaK and the LHCI subunit Lhca2 were at rather similar level as in WT (Figure 1A, B, C). Between plants of different age, only negligible differences were observed in the accumulation of representative subunits of the thylakoid membrane protein complexes (Figure 1A). Bearing this in mind, the subsequent experiments were performed with six-week-old WT and *var1* plants and eight-week-old *var2* plants to gain more leaf material of *var2*.

Uneven accumulation of PSI subunits observed in *var1* and *var2* as compared to WT (Figure 1B) was studied further using 2D blue native polyacrylamide gel electrophoresis (BN-PAGE) in combination with SYPRO ruby protein gel stain, which allows linear quantitation of distinct subunits within the protein complex. To that end, thylakoid membrane was solubilized by n-dodecyl β-D-maltoside, individual subunits of the protein complexes were separated by 2D BN-PAGE gels and protein spots were stained with SYPRO ruby protein gel stain. Interestingly, the abnormal stoichiometry of the integral components of PSI-LHCI was evident in both *var1* and *var2* thylakoids (Supplementary figure 2). Indeed, the densitometry of SYPRO stained PSI-LHCI complex revealed that the ratio of PsaH to PsaD (well-separated subunits were selected for quantification in order to avoid overlapping of the protein spots) in WT PSI-LHCI complex was 33% ± 3% whereas both *var1* and *var2* demonstrated only half (16% ± 5-6%) of the WT ratio. These results strongly imply that the subunit abundance of the PSI-LHCI complex differs between the WT and *var1* and *var2* plants.

2.2. Accumulation of PSI (sub)complexes in *var1* and *var2* thylakoids

Next, we addressed the amount of low molecular mass PSI complexes, which might represent either degradation products or biogenesis intermediates, in the *var1* and *var2* plants. The thylakoid membranes of the wild-type, *var1* and *var2* plants were solubilized using digitonin and the samples were submitted to separation of the protein complexes by a large pore blue native polyacrylamide gel electrophoresis (lpBN-PAGE). Digitonin was used as detergent as it solubilizes preferably PSI (Anderson and Boardman, 1966). To avoid accumulation of the PSI-LHCI-LHCII complex, dark-adapted plants were used for the experiment (Pesaresi et al., 2009). Immunoblotting of the native gels with a PsaB specific antibody revealed low accumulation of both PSI-LHCI and PSI core subcomplex in the mutant thylakoids as compared to WT (Figure 2). Similar co-regulation of the PSI-LHCI complex and PSI core subcomplex was reported earlier for an Arabidopsis mutant, which lacks the PSI assembly factor PSA2 (Fristedt et al., 2014).

2.3. Photosynthetic electron transfer in *var1* and *var2* plants under ML intensities

Next, the functional status of the photosynthetic apparatus was investigated in detail in the *var1* and *var2* mutants grown under moderate light conditions. The maximum quantum

yield of PSII in dark-adapted (F_V/F_M) and in light-adapted ($F_{V'}/F_{M'}$) leaves, did not show any statistically significant difference between *var1, var2* and WT (Table I). More detailed analyses of PSII acceptor side properties, measured as flash-induced increase and subsequent relaxation of Chl fluorescence yield (FF-relaxation) from the WT, *var1* and *var2* plants, gave likewise very similar results (Figure 3A). Collectively, these results strongly suggest the presence of unaffected PSII in *var1* and *var2* upon growth of plants under moderate light intensities. This differs drastically from high light conditions that induce severe PSII photoinhibition in the *var1* and *var2* plants, evidenced as a decrease in the F_V/F_M parameter (Bailey et al., 2002; Sakamoto et al., 2003). However, the effective quantum yield of PSII (Φ_{II}) measured under moderate actinic light intensities was significantly lower in the *var1* and *var2* mutant plants (0.30 ± 0.03 and 0.37 ± 0.04, respectively) compared to the WT (0.50 ± 0.08). The decrease in Φ_{II}, representing the fraction of absorbed energy utilized by photochemistry, could originate from an increase in the yield of regulated protective non-photochemical energy dissipation, Φ_{NPQ}, and/or in the yield of non-regulated non-photochemical energy loss, Φ_{NO}, reflecting the fraction of energy that is passively dissipated in the form of heat and fluorescence, mainly due to closed PSII reaction centers (Hendrickson et al., 2004; Kramer et al., 2004). There was no statistically significant difference in Φ_{NO} values between the wild-type and mutant plants (Table I). However, a decrease in the Φ_{II} was accompanied by considerable increase of the Φ_{NPQ} in *var1* and *var2* (0.44 ± 0.03 and 0.39 ± 0.04, respectively), as compared to the WT (0.22 ± 0.10) (Table I). Induction kinetics of significantly higher NPQ level in the *var1* and *var2* lines compared to the WT is also depicted in the Figure 3B. The excitation pressure of PSII (1-qP), which reflects the redox state of the plastoquinone pool was slightly higher in *var1* as compared to WT, whereas no statistically significant difference was recorded between *var2* and WT.

Contrary to the similar F_V/F_M values between *var1, var2* and WT, lack of either FtsH2 or FtsH5 had a drastic effect on P_M, the PSI parameter representing the maximum amount of photo-oxidizable P_{700}. The P_M values of the light-acclimated leaves of both *var1* and *var2* (0.60 ± 0.07 and 0.48 ± 0.17, respectively) were significantly lower as compared to the WT (0.89 ± 0.14) indicating a low amount of photo-oxidizable P_{700} in both mutant lines (Table I). Moreover, the performance of PSI under actinic light, measured as effective quantum yield of PSI (Φ_I), was significantly lower in *var1* and *var2* (0.47 ± 0.04 and 0.62 ± 0.05, respectively) as compared to the WT (0.77 ± 0.04). The drop in the Φ_I value can be attributed to the donor

(Φ_{ND}) and/or the acceptor side (Φ_{NA}) limitation of PSI. In both mutant lines a significant donor side limitation of PSI was recorded, whilst no limitation on the acceptor side of PSI was evident between mutant lines and the WT (Table I).

Moreover, re-reduction of P_{700} in darkness, after termination of far red light, was faster in both *var1* and *var2* mutants than in WT (Figure 3C). This result implied a high capacity of the *var1* and *var2* plants for PSI cyclic electron transfer (CET) followed by protonation of the lumen, which is a prerequisite for triggering of NPQ and a photosynthetic control of the Cyt b_6f complex.

2.4. Biosynthesis of PSI is impaired in *var1* and *var2* plants under ML intensities

Scarcity of PSI in the *var1* and *var2* lines (Figure 1, Table I) could originate either from accelerated damage to PSI or serious defects in biosynthesis of PSI. Thus, we next focused on both the biosynthesis and degradation of PSI complexes in the thylakoid membrane of WT, *var1* and *var2* plants. Based on RNA blot with specific probes, it was demonstrated that the mRNAs (*psaA-psaB-rps14*) encoding the PsaA/PsaB proteins accumulated in higher amount in *var1* and in similar amount in *var2* as in the WT plants (Figure 4A), when loading was done based on the total RNA. Next, the efficiency of translation initiation of the *psaA/B* mRNAs was assessed by a polysome loading experiment. Following the migration of the mRNA-ribosome complexes in sucrose gradient upon ultracentrifugation revealed only a slight shift between mutant and WT plants in the polysome loading efficiency of the *psaA/B* mRNAs (Figure 4B). In line with this, polysome profiles of *psbA* and *psbD* mRNAs were similar in WT and the *var* mutant plants (Supplementary figure 3). It should be noted that normalization in the polysome loading experiment was performed on the basis of fresh weight of samples and the presence of white sectors affected the amount of *psaA/B* mRNA in variegated plants as compared to the RNA blot experiment. Collectively, the mRNA and polysome loading results implicate that the failure to accumulate the PsaB protein in *var1* and *var2* mutants is likely not linked to the *psaA/B* transcription efficiency, mRNA stability or translation initiation of the PsaB protein.

Remaining options for reduced PsaB accumulation in *var1* and *var2* as compared to WT plants included differences in translation efficiency and stability of the PsaB protein. In order

to dissect between these two possibilities, we applied *in vivo* pulse-chase labeling experiments using ^{35}S-methionine. The newly-synthetized proteins were identified by 2D BN-PAGE separation of the WT pulse samples solubilized with n-dodecyl β-D-maltoside. PsaA/B proteins were found to migrate slightly above the ATP synthase subunits in the BN-PAGE autoradiogram films (Supplementary figure 4, for mass spectrometric identification (Aro et al., 2005). Synthesis and degradation of the PsaA/B proteins were followed by separation of the ^{35}S-methionine labeled proteins by 1D SDS-PAGE (Figure 4C). For optimal separation of the α and β subunits of ATP synthase from the PsaA/B proteins, the running time in the SDS-PAGE gels was extended from that used for BN-PAGE and presented in the Supplementary figure 4.

As demonstrated in Figure 4C, the *var1* and *var2* plants accumulated clearly less radioactivity in the PSI reaction center proteins PsaA/B than the WT plants, evidenced by denaturing SDS-PAGE of thylakoid membrane proteins after ^{35}S-methionine labeling of the leaves for five min and 20 min. Such short labeling times allowed discrimination between possible defects in biosynthesis (faster process) and degradation (slower process) of the PSI core proteins. In order to determine the relative synthesis rate of the PsaA/B proteins (calculated as the amount of radioactivity incorporated into the PsaA/B proteins relative to that incorporated into the ATPβ and D1 proteins), a longer duration of ^{35}S-methionine labeling of the leaves (2h) was applied in order to accumulate more newly-synthetized radiolabeled PsaA/B proteins. These samples were also further chased for two hours in the presence of non-radioactive methionine to estimate the degradation rates of the PsaA/B proteins. The calculated relative synthesis rates of the PsaA/B proteins were only 37% ± 8% in *var1* and 31% ± 11% in *var2* of that recorded for the WT plants (n=3). Instead, no drastic differences between the WT and mutant plants were observed in degradation of the newly-synthetized PsaA/B proteins during the 2h chase period (Figure 4C). However, the exact evaluation of the degradation rate of PSI core proteins in mutants was not possible due to a low incorporation of radioactivity into the newly-synthetized PsaA/B proteins (i.e. a low synthesis rate) in the *var1* and *var2* plants.

To fully exclude the possibility that the scarcity of PSI in *var1* and *var2* originated from abnormally fast degradation of the complex under ML conditions, we applied lincomycin, a chloroplast translation inhibitor, to compare the degradation of the D1 protein and the PsaB protein between the *var1*, *var2* and WT plants. In line with the pulse-chase labeling

277 experiments, no statistically significant difference in the amount of PsaB (and D1) was
278 recorded in *var1*, *var2* and WT leaves up to eight hours of exposure to ML in the presence of
279 lincomycin (Figure 5A, B). On the contrary, under high intensity light (800 µmol photons $m^{-2}s^{-1}$)
280 the lincomycin-treated *var1* and *var2* plants, as expected (Lindahl et al., 2000; Bailey et
281 al., 2002), could not properly degrade the D1 protein, as occurred in the WT (Figure 5C).
282 Although under high light intensity and in the presence of lincomycin, the PsaB protein
283 degraded slightly faster in the mutant plants as compared to WT, the results in Figure 5 do
284 not support superior degradation of PsaB in *var* mutants under ML conditions (Figure 1). We
285 thus conclude that the scarcity of PSI in *var1* and *var2* did not originate from instability of
286 the PsaB, but rather arised from low translation efficiency of the PSI core proteins.
287
288 2.5. PSI assembly factors in WT, *var1* and *var2* plants under ML intensities
289
290 Defects in biosynthesis of thylakoid protein complexes have earlier been shown to influence
291 the accumulation of auxiliary proteins assisting the assembly of the same complex (Cai et al.,
292 2010). To address this, we first analysed an accumulation of two well-known PSI assembly
293 factors, Y3IP1 and Ycf4, in the thylakoid membrane of *var1* and *var2*. Y3IP1 (Albus et al.,
294 2010) accumulated in *var1* in high amount but was less abundant in *var2* as compared to WT
295 (Figure 6). Instead, Ycf4 (Krech et al., 2012) was present in high amounts in both *var1* and
296 *var2* mutants. Unlike the PSI assembly factors, no distinct differences occurred in the
297 accumulation of PSII auxiliary proteins, LPA1, LPA2 and TLP18.3 (Peng et al., 2006; Ma et
298 al., 2007; Sirpiö et al., 2007) between WT, *var1* and *var2*. Instead, the amount of CYP38 (Fu
299 et al., 2007) was higher in both *var* mutant plants as compared to WT. It should be noted,
300 however, that even if CYP38 is referred to as an auxiliary protein of PSII, *cyp38* plants
301 contain low amount of also PSI (Sirpiö et al., 2008), similar to the *var1* and *var2* mutants.
302
303 **3. Discussion**
304
305 Type A and type B FtsH isomers have been identified in cyanobacteria, green and red algae,
306 mosses and flowering plants (Kato et al., 2012a). The *var1* mutant is deficient of the type A
307 FtsH isomer FtsH5 and *var2* of the type B FtsH isomer FtsH2. Importantly, type A isomer
308 FtsH1 and type B isomer FtsH8 can substitute FtsH5 and FtsH2, respectively, and therefore
309 the *var1* and *var2* are, in practice, FtsH knock-down lines (Figure 1A) (Zaltsman et al.,
310 2005b). The FtsH proteins play a crucial role in proteolysis of membrane-embedded proteins,

311 including the photodamaged PSII reaction center protein D1 (Lindahl et al., 2000; Bailey et
312 al., 2002; Sakamoto et al., 2003). Thylakoid-bound FtsH proteases have likewise been shown
313 to participate in quality control of the Cyt b_6f complex (Ostersetzer and Adam, 1997; Malnoë
314 et al., 2014) and possibly in regulation of the PSI CET (Terashima et al., 2012; Szyszka-Mroz
315 et al., 2015). Here we demonstrate that FtsH2 and FtsH5 also play an important role in
316 biosynthesis of PSI complex.
317
318 Under ML conditions, lower amount of the FtsH proteases in the *var1* and *var2* mutant plants
319 do not impair the function or turnover of the PSII complex (Figure 1A, Figure 3A, Table I).
320 This corroborates with earlier reports (Sakamoto et al., 2003; Zhang et al., 2010) and
321 indicates that the photodamaged PSII is efficiently restored by a rapid PSII repair cycle in the
322 WT as well as in the *var1* and *var2* plants under ML intensities. The low values of effective
323 PSII quantum yield (Φ_{II}) in the *var1* and *var2* mutants is not related to the PSII
324 photoinhibition, but rather stems from a highly elevated NPQ (Φ_{NPQ}) yield (Table I, Figure
325 3B).
326
327 Contrary to the PSII complex, whose function is fully secured in the absence of FtsH2 or
328 FtsH5 under ML intensity, the PSI complex turned out to be significantly affected under the
329 same conditions. Interestingly, the amount of PSI, evidenced by both biochemical (Figure
330 1A) and biophysical (P_M value, Table I) measurements, was directly proportional to the
331 amount of the thylakoid-bound FtsH proteins in *var1* and *var2*. Low amount of PSI observed
332 in the mutant lines was somewhat surprising, considering earlier reports showing similar
333 amount of PsaF subunit in *var2* as compared to that of WT (Yu et al., 2008; Yu et al., 2011).
334 Nonetheless, our data suggest that in the *var1* and *var2* several low molecular mass nuclear-
335 encoded PSI subunits (PsaD, PsaK, Lhca2) are present in high amounts within the PSI-LHCI
336 complex (Figure 1, Supplementary figure 2). Such non-stoichiometric amount of different
337 PSI subunits has been observed also earlier in various PSI mutants. *Nicotiana tabacum*
338 Y3IP1-1 suppression line accumulates more PsaD as compared to PSI core (Albus et al.,
339 2010) and *Chlamydomonas reinhardtii* (Chlamydomonas) F15 mutant deficient of TAB1
340 (deficient in translation of the *psaB* mRNA) is capable of accumulating PsaD and PsaF to
341 some extent, despite total absence of the PSI core (Boudreau et al., 1997). Similarly, high
342 accumulation of LHCI as compared to the PSI core is a well-known phenomenon within the
343 PSI auxiliary protein mutants (Amann et al., 2004; Lezhneva and Meurer, 2004; Lezhneva et

al., 2004). The reason behind non-stoichiometric accumulation of low molecular mass subunits of PSI as compared to PSI core in the PSI auxiliary protein mutants is currently not known and more efforts are needed to unravel the underlying mechanisms behind the phenomenon.

Scarcity of PSI in *var1* and *var2* under ML conditions (Figure 1, 2, Table I) could, in theory, originate either from serious damage to PSI or defects in the biosynthesis of PSI. In general, PSI can suffer from irreversible photoinhibition under conditions where the PSI acceptor side is overreduced, leading to formation of reactive oxygen species, which in turn damage the Fe-S centers of PSI (Inoue et al., 1986; Sonoike et al., 1995; Tiwari et al., 2016). However, no acceptor side limitation of PSI could be revealed in the *var1* and *var2* mutants, but instead, the PSI donor side was shown to be more oxidized in both the *var1* and *var2* mutants than in WT, which, in turn, led to decreased effective quantum yield of PSI, Φ_I (Table I). We assume that during induction of photosynthesis a high CET around PSI is likely to trigger a strong acidification of lumen and thus also higher NPQ by concomitantly inducing a significant photosynthetic control of electron flow via the Cyt b_6f complex (Joliot and Johnson, 2011) in the *var1* and *var2* mutants (Table I, Figure 3B). This, in turn, decreases the electron supply to P700, which leads to the donor side limitation of PSI in both the *var1* and *var2* mutants under steady-state illumination. Importantly, PSI CET was assessed as P_{700} re-reduction kinetics conducted in darkness after shutting off the far-red light, which preferentially excites PSI. Therefore the measurement setting does not mimic the growth condition, where the leaves are illuminated by continuous white light, but rather reflects a maximum CET capacity of the leaves during induction of photosynthesis. In line with these results, the PSI core does not show accelerated photodamage and degradation in *var1* or *var2* plants under ML conditions (Figure 4C, 5).

Our results provide evidence that the deficiency of the FtsH2 and FtsH5 proteases impairs the translation efficiency of the PsaA/B proteins (Figure 4). Several reports have provided information, which indicates that the role of FtsH during the biogenesis of PSI might be direct. Indeed, FtsH2 has been observed to be attached to the thylakoid associated polysomes, which are responsible for translation of chloroplast-encoded membrane proteins like PsaA/B (Sirpiö et al., 2007). Further, *var2* suppressor screens have shown that the decreased translation rate caused by the secondary mutation on *var2* background leads to proper

chloroplast development (Liu et al., 2013; Putarjunan et al., 2013), which indicates that the functional role of FtsH2 is linked to the chloroplast translation machinery. Moreover, the chloroplast-encoded PSI assembly factor Ycf4 accumulated in high amounts in the *var1* and *var2* plants (Figure 6), similar to a PSI mutant characterised by reduced translation efficiency of the *psaA* mRNA (Krech et al., 2012). On the other hand, modified electron transfer (Table I, Figure 3) and/or accumulation of ROS (Kato et al., 2009) in *var1* and *var2* plants might also hamper the translation of PsaA/B mRNA. Further, a low amount of Y3IP1 has been shown to be connected with a deficiency in PSI (Albus et al., 2010), being in line with a lower amount of both Y3IP1 and PSI in *var2* than in *var1* (Figures 1, 6). Whether the thylakoid-bound FtsHs have a direct role during the translation elongation of PSI core protein still remains to be verified.

If the role of FtsH in the biogenesis of PSI is direct, it would be interesting to know whether the thylakoid-bound FtsH functions as a structural scaffold or as a protease during the synthesis of the PSI core. Previous report has shown that the protease activity of type B isoform of FtsH is unnecessary for chloroplast biogenesis (Zhang et al., 2010), which indicates either redundancy of protease sites or function of FtsH as a chaperone. Translation of the PsaA/B proteins is down-regulated in *var* mutant plants (Figure 4C), which suggests a role for FtsH as a structural scaffold. Also accumulation of the PSI assembly factors in *var1* and *var2* as a compensatory mechanism (Figure 6) is an indirect evidence supporting it´s role as a chaperone. However, we cannot exclude the possibility that thylakoid-bound FtsHs play a role in degradation of low molecular mass PSI subunits, like PsaD or PsaK (Figure 1). To that end, the role of FtsH as a protease ensuring the quality control during biogenesis of PSI is also possible. In *E. coli* (*Escherichia coli*) FtsH has long been known to be responsible for both the proteolysis of unassembled DrrB (bacterial doxorubicin resistance protein B) protein and the refolding of misassembled DrrAB (Akiyama et al., 1994; Li et al., 2013). In addition, Arabidopsis Deg1 protease was earlier shown to be involved both in the degradation of damaged D1 protein and in the assembly of the PSII complex (Sun et al., 2010).

Further support for thylakoid-bound FtsH proteins as important auxiliary proteins for proper biosynthesis of PSI comes from cyanobacteria research. Disruption of *slr0228*, encoding one of the four putative homologues of FtsH in *Synechocystis* sp. PCC 6803, was found to cause major reduction in the abundance of PSI, without affecting the cellular content of PSII or phycobilisomes (Mann et al., 2000). The *slr0228* gene encodes an FtsH isomer that belongs

411 to type B FtsHs together with Arabidopsis FtsH2 (Kato et al., 2012a). Moreover, in the
412 Chlamydomonas *ftsh1-1* mutant the amount of PsaA was shown to be drastically down-
413 regulated, when cells were grown mixotrophically under 50 or 150 µmol photons $m^{-2}s^{-1}$,
414 while the amount of PsaD and PsaL remained unaltered as compared to the WT cells
415 (Malnoë, 2011). Similar function of FtsH in *Synechocystis* sp. PCC 6803, Chlamydomonas
416 and Arabidopsis provides evidence that the function of FtsH in biosynthesis of PSI is
417 evolutionarily conserved in oxygenic photosynthetic organisms.
418
419 Finally, the difference in accumulation of FtsH in *var2* and *var1* is likely to explain the
420 specific modifications of the photosynthetic electron transfer and varying accumulation of
421 PSI auxiliary proteins in the two *var* mutants (Table I, Figure 6). Moreover, it is plausible
422 that not only the quantity of FtsH matters but the FtsH isomers type A and type B possibly
423 play partially different roles in the thylakoid membrane, also independently of the hetero-
424 hexameric FtsH protease complex. Indeed, it was previously reported that specifically the
425 *var1* mutant plants show a distinct temperature sensitive phenotype (Sakamoto et al., 2002).
426 To that end, the future goal is to reveal in detail the multitude of functions carried out by the
427 thylakoid-bound FtsH proteins during the entire life cycle of the chloroplast.
428
429 **4. Conclusions**
430
431 We show here that the FtsH proteins are of utmost importance for proper biosynthesis of PSI
432 under normal growth conditions, whilst at high light conditions the function of FtsH proteins
433 in degradation of damaged D1 reaction center proteins of PSII becomes dominant. In line
434 with these two most important roles of FtsH, the high light treatment has been shown to lead
435 to a migration of FtsH from stroma lamellae, where PSI is mainly located, to grana margins,
436 where D1 degradation is likely to take place (Puthiyaveetil et al., 2014). So far, the origin of
437 the variegation phenotype of the FtsH2 and FtsH5 deficient plants has remained unknown. To
438 that end, our current results raise a question whether the variegation phenotype of the *var2*
439 and *var1* mutants might partially result from problems in translation of the PSI core proteins?
440 It is clear that defective PSI biosynthesis *per se* does not lead to variegation phenotype but it
441 might be one of the factors, which determine the threshold of FtsH activities necessary for
442 proper chloroplast development.
443
444 **5. Materials and methods**

445

446 5.1. Plant material and growth conditions

447

448 Six-week-old or eight-week-old Arabidopsis (*Arabidopsis thaliana*), ecotype Columbia 0
449 WT, *var1-1* (NASC seed line N271), *var2-2* (NASC seed line N272), plants were used for
450 most of the experiments. Plants were grown under a photon flux density of 120 µmol photons
451 $m^{-2}s^{-1}$ in 8h light regime at 23ºC. For specific experiment, plants were shifted to high
452 intensity light (800 µmol photons $m^{-2}s^{-1}$) up to three hours. Osram HQI-BT 400 W/D Metal
453 Halide lamps were used as light source. Oldest and youngest rosette leaves were excluded
454 from the experiments. In experiments with inhibition of translation, 1 mM lincomycin was
455 incorporated into leaves through petioles overnight.

456

457 5.2. Isolation of the thylakoid membrane

458

459 Leaves were grinded in ice-cold grinding buffer (50 mM HEPES–KOH, pH 7.5, 330 mM
460 sorbitol, 2 mM EDTA, 1 mM $MgCl_2$, 5 mM ascorbate, 0.05% (w/v) bovine serum albumin,
461 10 mM NaF) and suspension was filtered through two layers of Miracloth and centrifuged at
462 5,000 g at 4°C for 4 min. Pellet was suspended in shock buffer (50 mM HEPES–KOH, pH
463 7.5, 5 mM sorbitol, 5 mM $MgCl_2$, 10 mM NaF) and centrifuged at 5,000 g at 4°C for 4 min.
464 Pellet was suspended into storage buffer (50 mM HEPES–KOH, pH 7.5, 100 mM sorbitol, 10
465 mM $MgCl_2$, 10 mM NaF) and centrifuged at 5,000 g at 4°C for 4 min. Finally the pellet was
466 resuspended into small aliquot of storage buffer. The Chl content was determined according
467 to Porra et al., 1989.

468

469 5.3.*In vivo* pulse labeling of thylakoid proteins

470

471 Radioactive methionine was incorporated into detached leaves through petioles (20 µCi ml^{-1}
472 [^{35}S] Methionine and 0.4% (v/v) Tween 20). The pulse labeling was performed at 23°C under
473 darkness (16 hours) followed by shift to 120 µmol photons $m^{-2}s^{-1}$ (5 min, 20 min and 2 h).
474 For chase experiment, the leaves were washed with unlabeled methionine (10 mM L-
475 methionine, 0.4% (v/v) Tween 20) followed by 1 hour incorporation of unlabeled methionine
476 under darkness. Chase experiment was performed under 120 µmol photons $m^{-2}s^{-1}$ at 23°C and
477 the samples were collected after two hours. The synthesis and degradation of the PsaA/B

proteins was followed using autoradiogram films. Quantification of different proteins was carried out by densitometry analysis of the films with FluorChemTM 8000 image analyzer (Alpha Innotech Corporation, San Leandro, CA, U.S.A.).

5.4. Separation and detection of thylakoid proteins and protein complexes

The polypeptides were separated with SDS-PAGE (12% polyacrylamide, 6 M urea) according to standard procedures. The proteins were electroblotted to a PVDF membrane (Millipore, Watford, Herts, UK) and immunodetected with protein specific antibodies. Gels were loaded on Chl basis. The lpBN-PAGE and BN-PAGE gels were performed essentially as described in Järvi et al., 2011. The thylakoid membrane (4-8 μg of Chl) was resuspended into ice-cold 25BTH20G buffer (25 mM BisTris/HCl (pH 7.0), 20% (w/v) glycerol and 0.25 mg ml^{-1} Pefabloc) to a Chl concentration of 1.0 mg ml^{-1}. An equal volume of detergent solution (diluted in 25BTH20G) was added to a final concentration of 1.0% (w/v) for DM (Sigma) or 2.0% (w/v) for digitonin (Calbiochem). Thylakoid membrane was solubilized in darkness for 5 min either on ice when using DM or at 20ºC with continuous gentle mixing when using digitonin. Traces of insoluble material were removed by centrifugation at 18,000 g at 4ºC for 20 min. Prior to loading, the samples were supplemented with a one-tenth volume of Serva Blue G buffer (100 mM BisTris/HCl (pH 7.0), 0.5 M ACA, 30% (w/v) sucrose and 50 mg ml^{-1} Serva Blue G). SYPRO®Ruby staining was performed according to Invitrogen Molecular Probes™ instructions.

5.5.Nucleic acid analyses

Total RNA was isolated from leaves of four-week-old plants as described in Armbruster et al., 2010. RNA gel blot analyses were performed under stringent conditions on 10-µg samples of total RNA according to Sambrook and Russell, 2001. Polysome analyses were performed as described in Barkan, 1988. Leaf tissue (200 mg) was frozen with liquid nitrogen and ground. Subsequently, the microsomal membranes were solubilized with 1% (v/v) Triton X-100 and 0.5% (w/v) sodium deoxycholate. The solubilized material was layered onto 15/55% sucrose step gradients (corresponding to 0.44/1.6 M sucrose) and centrifuged at 250,000 g at 4°C for 65 min. The step gradient was fractionated in 12 aliquots and the mRNA associated with polysomes was extracted with phenol/chloroform/isoamyl alcohol (25:24:1), followed by precipitation at room temperature with 95% ethanol. All samples were then

subjected to RNA gel blot analysis. Methylene blue stained membranes were used as loading controls. Probes complementary to chloroplast genes were exploited for the hybridizations. All probes used were cDNA fragments labelled with 32P.

5.6. Photosynthetic activity measurements

The Dual-PAM-100 (Walz, http://www.walz.com/) was used for the simultaneous *in vivo* measurement of PSII and PSI photosynthetic parameters, based on Chl *a* fluorescence and P_{700} absorption changes (difference of intensities of 875 and 830 nm pulse-modulated measuring light reaching the photodetector) (Klughammer and Schreiber, 2008), respectively. The red light irradiation of 120 µmol photons m^{-2} s^{-1} was used as an actinic light. Saturating pulse (800 ms, 6000 µmol photons m^{-2} s^{-1}) was applied to determine the maximal fluorescence. Maximum quantum yield of PSII ($(F_M-F_0)/F_M = F_V/F_M$, and $(F_{M'}-F_{0'})/F_{M'} = F_{V'}/F_{M'}$), effective quantum yield of PSII (Φ_{II}), the quantum yields of non-photochemical energy conversion in PSII (Φ_{NPQ} and Φ_{NO}) and the excitation pressure (1-qP) of PSII were determined from leaves dark adapted for 30 min before the measurements. PSI quantum yield, Φ_I, and complementary PSI quantum yields, Φ_{ND} and Φ_{NA}, were measured from light adapted leaves to eliminate the PSI acceptor side limitation by dark inhibition of Calvin-Benson cycle. In order to determine P_M value, a maximal change of the P_{700} signal from the fully reduced to the fully oxidized state, light adapted leaves were illuminated with far-red light for 10 s, and the saturating pulse (5000 µmol photons $m^{-2}s^{-1}$) was applied for 300 ms. For determination PSI CET, P_{700} was oxidized by far-red light for 30 s, and the subsequent re-reduction of P_{700}^+ in darkness was monitored. The flash-induced increase and the subsequent decay of Chl fluorescence yield was measured using fluorometer FL 3500 (PSI Instruments). Leaves were dark adapted for three min before the excitation with a strong single-turnover flash.

5.7. Statistical Analyses

The numerical data were subjected to statistical analysis by Student's t test with statistical significance at the p values < 0.05.

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Author contributions:

S. J., M.S., Y.A. and E.-M.A. designed the research. S.J., M.S., A.I., L.T. and S.R. performed the research. S. J., M.S., D.L., Y.A. and E.-M.A. analyzed the data and wrote the article.

Tables:

Table I. Functional characteristics of the thylakoid membrane of WT, *var1* and *var2* plants. Values were measured from plants grown under moderate light intensities (120 μmol photons $m^{-2}s^{-1}$).

Photosynthetic parameter	Col-0	*var1*	*var2*
Fraction of oxidizable PSI, P_M	0.89±0.14	0.60±0.07*	0.48±0.17*
Effective PSI quantum yield, Φ_I	0.77±0.04	0.47±0.06*	0.62±0.05*
PSI donor side limitation, Φ_{ND}	0.12±0.05	0.42±0.07*	0.29±0.06*
PSI acceptor side limitation, Φ_{NA}	0.11±0.05	0.11±0.02	0.09±0.07
Maximal quantum yields of PSII,			
F_V/F_M	0.80±0.03	0.81±0.02	0.78±0.05
$F_{V'}/F_{M'}$	0.63±0.09	0.61±0.10	0.54±0.14
Effective PSII quantum yield, Φ_{II}	0.50±0.08	0.30±0.03*	0.37±0.04*
Non-photochemical energy dissipation, Φ_{NPQ}	0.22±0.10	0.44±0.03*	0.39±0.04*
Yield of non-regulated non-photochemical energy loss, Φ_{NO}	0.28±0.04	0.26±0.02	0.24±0.05
Excitation pressure of PSII, 1-qP	0.37±0.06	0.51±0.06*	0.41±0.05

The values are the means ± SD, n = 7-10. Statistically significant differences comparing the mutant plants to that of the corresponding WT are marked with asterix (*). See text for details. Col-0, wild-type.

563 **Figure legends:**

564

565 Figure 1. Accumulation of thylakoid proteins in *var1*, *var2* and wild-type plants grown under
566 moderate light intensities (120 µmol photons $m^{-2}s^{-1}$). A. Immunoblots of the thylakoid
567 membrane proteins isolated from 6-week-old and 8-week-old plants. B. Immonoblots of the
568 various PSI subunits. C. Quantification of PSI subunits in *var1* and *var2* as compared to wild
569 type (error bars indicate SD, statistically significant differences are marked with asterisk (*)).
570 Gels were loaded on Chl basis. A representative example from three independent biological
571 replications is shown. Col-0, wild type.

572

573 Figure 2. Accumulation of PSI complexes in *var1*, *var2* and wild-type plants. Thylakoids
574 were isolated at the end of the dark period, solubilized with digitonin and protein complexes
575 were separated by large pore blue native (lpBN)-PAGE analysis. Gels were loaded on Chl
576 basis. PSI complexes were identified by PsaB antibody. A representative example from three
577 independent biological replications is shown. Col-0, wild type.

578

579 Figure 3. Flash-induced increase and subsequent relaxation of the chlophyll fluorescence
580 yield (FF-relaxation), non-photochemical quenching (NPQ) and re-reduction of P_{700}^{+} in
581 darkness in wild type (black line), *var1* (grey line) and *var2* (pale grey line). A. FF-relaxation
582 in darkness. Curves, representing average of 32 independent measurements, are normalized to
583 the same amplitude for direct comparison of the kinetics. B. Induction and relaxation of NPQ
584 monitored during dark-to-light transition (120 µmol photons $m^{-2}s^{-1}$). Light period (white bar),
585 dark period (black bar). Curves represent an average of six independent measurements. C.
586 Re-reduction of P_{700}^{+} in darkness. P_{700} was oxidized by illumination of the leaf with far red
587 (FR) light for 30s and after termination of FR illumination, $P700^{+}$ re-reduction was monitored
588 in darkness. Curves, representing an average of six independent measurements, are
589 normalized to the same amplitude for direct comparison of the kinetics. Col-0, wild type.

590

591 Figure 4. Biogenesis and degradation of PsaA/B in *var1*, *var2* and wild-type plants. A. RNA
592 blot analysis of mRNAs encoding PSI core proteins. B. Association of mRNAs encoding PSI
593 core proteins with polysomes. Polysomes were fractionated using ultracentifugation, mRNAs
594 were separated by agarose gel electrophoresis and specific probes were used to identify
595 mRNA. C. *In vivo* pulse labeling. Leaves were labeled under moderate light for five min and
596 20 min (left panel) or for two hours followed by two hours chase in the presence of unlabeled

methionine (right panel). [35S] methionine labeled proteins were separated by SDS-PAGE. Synthesis and degradation of the PsaA/B proteins was followed using autoradiogram films. A representative example from three independent biological replications is shown. Col-0, wild type; M.B. methylene blue.

Figure 5. Degradation of D1 and PsaB proteins in the lincomycin treated *var1*, *var2* and wild-type leaves. 1mM lincomycin (lin) was incorporated into detached leaves trough petioles overnight in darkness. Prior to thylakoid isolation leaves floating on water were shifted from darkness to A. and B. moderate light (ML, 120 µmol photons $m^{-2}s^{-1}$) or C. high light (HL, 800 µmol photons $m^{-2}s^{-1}$). A. and C. Immunoblot analysis of degradation of D1 and PsaB proteins. B. Relative amounts of the D1 and PsaB proteins in wild type, *var1* and *var2* after the light treatments of leaves (as indicated in the figure B) and expressed as a proportion of respective dark controls (error bars indicate SD). Gels were loaded on equal Chl basis. Col-0, wild type.

Figure 6. Accumulation of the PSI and PSII auxiliary proteins in the *var1*, *var2* and wild-type plants. Immunoblots of the thylakoid membrane proteins separated by SDS-PAGE. Gels were loaded on Chl basis. A representative example from three independent biological replications is shown. Col-0, wild type

Supplementary figure 1. Phenotype of the *var1*, *var2* and wild-type plants. Plants were grown under moderate light intensities (120 µmol photons $m^{-2}s^{-1}$). Photograph was taken from 6-week-old plants.

Supplementary figure 2. 2D blue native (BN)-PAGE analysis of individual subunits of the PSI complex. Thylakoid membrane is solubilized with n-dodecyl β-D-maltoside, separated by 2D BN-PAGE and protein spots are stained with SYPRO ruby protein stain. Gels were loaded on Chl basis. The proteins are identified based on (Aro et al., 2005). PSI core proteins are marked with circles and low molecular mass subunits with arrows. A representative example from two independent biological replications is shown. Col-0, wild type.

Supplementary figure 3. Association with polysomes of the mRNAs encoding PSII core proteins PsbA and PsbD. Polysomes were fractionated using ultracentifugation, mRNAs were

630 separated by agarose gel electrophoresis and specific probes were used to identify mRNAs. A
631 representative example from two (PsbD) or three (PsbA) independent biological replications
632 is shown. Col-0, wild type.
633
634 Supplementary figure 4. 2D blue native (BN)-PAGE analysis of thylakoid membrane proteins
635 after pulse labeling. Wild-type Arabidopsis leaves were labeled under moderate light (120
636 μmol photons $m^{-2}s^{-1}$) for two hours with [35S] methionine. Thylakoid membrane is
637 solubilized with n-dodecyl β-D-maltoside, separated by 2D BN-PAGE and protein spots are
638 visualized using autoradiogram films. A representative example from three independent
639 biological replications is shown.
640
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Figure 1

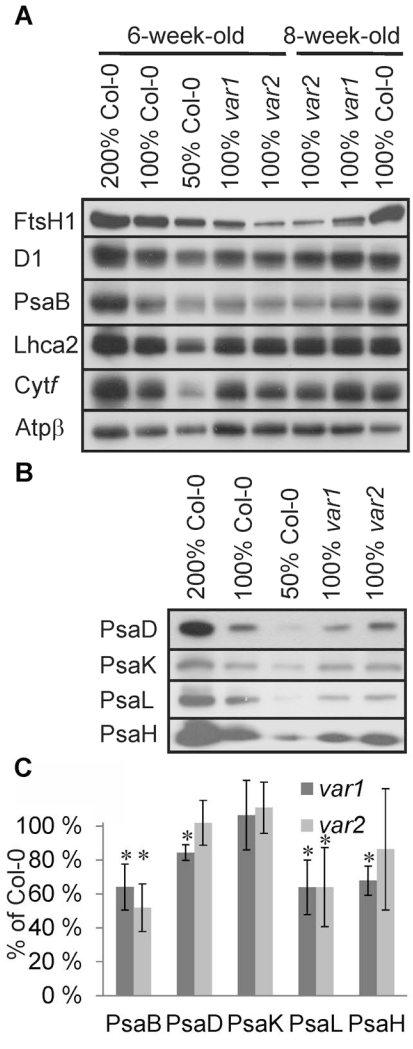

Figure 1. Accumulation of thylakoid proteins in *var1*, *var2* and wild-type plants grown under moderate light intensities (120 µmol photons $m^{-2}s^{-1}$). A. Immunoblots of the thylakoid membrane proteins isolated from 6-week-old and 8-week-old plants. B. Immonoblots of the various PSI subunits. C. Quantification of PSI subunits in *var1* and *var2* as compared to wild type (error bars indicate SD, statistically significant differences are marked with asterisk (*). Gels were loaded on Chl basis. A representative example from three independent biological replications is shown. Col-0, wild type.

Figure 2

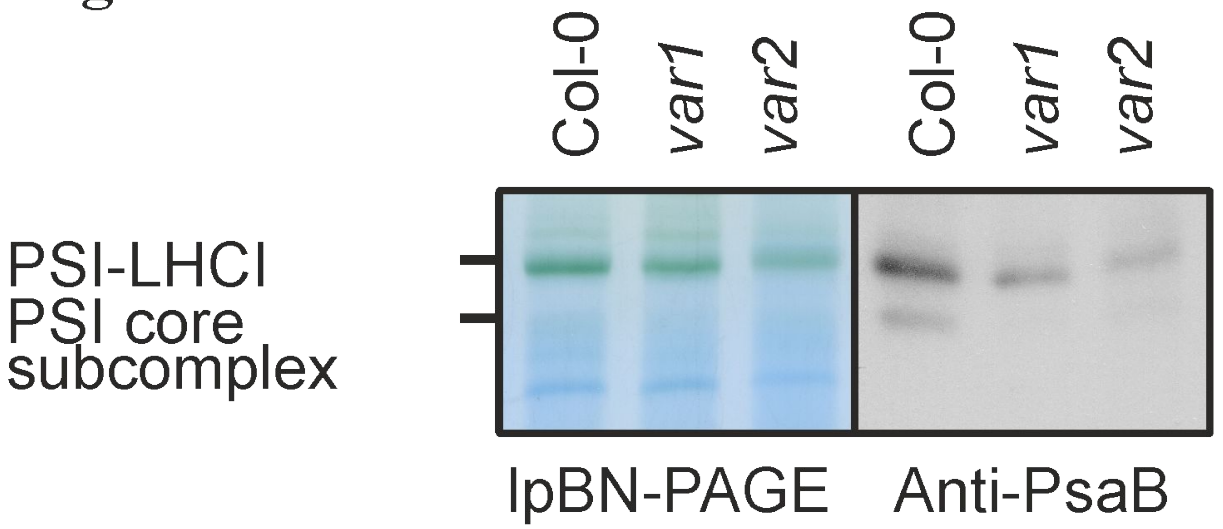

Figure 2. Accumulation of PSI complexes in *var1*, *var2* and wild-type plants. Thylakoids were isolated at the end of the dark period, solubilized with digitonin and protein complexes were separated by large pore blue native analysis. Gels were loaded on Chl basis. PSI complexes were identified by PsaB antibody. A representative example from three independent biological replications is shown. Col-0, wild type.

Figure 3

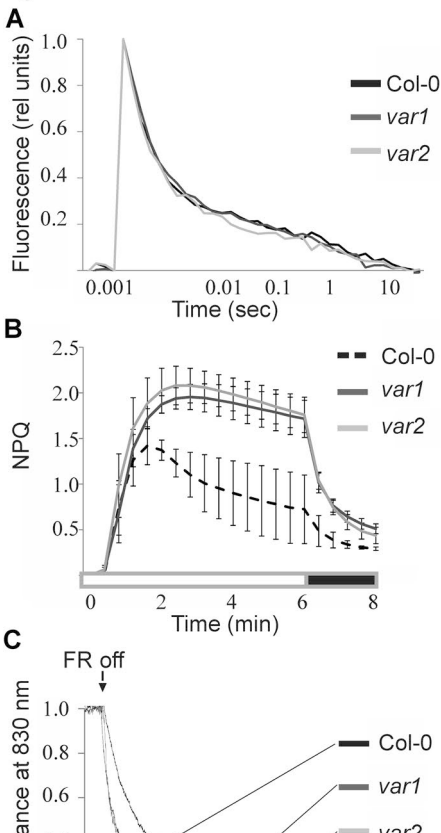

Figure 3. Flash-induced increase and subsequent relaxation of the chlophyll fluorescence yield (FF-relaxation), non-photochemical quenching (NPQ) and re-reduction of P_{700}^{+} in darkness in wild type (black line), *var1* (grey line) and *var2* (pale grey line). A. FF-relaxation in darkness. Curves, representing average of 32 independent measurements, are normalized to the same amplitude for direct comparison of the kinetics. B. Induction and relaxation of NPQ monitored during dark-to-light transition (120 µmol photons m^{-2} s^{-1}). Light period (white bar), dark period (black bar). Curves represents an average of six independent measurements. C. Re-reduction of P_{700}^{+} in darkness. P_{700} was oxidized by illumination of the leaf with far red (FR) light for 30 s and after termination of FR illumination, P_{700}^{+} re-reduction was monitored in darkness. Curves, representing an average of six independent measurements, are normalized to the same amplitude for direct comparison of the kinetics. Col-0, wild type.

Figure 4

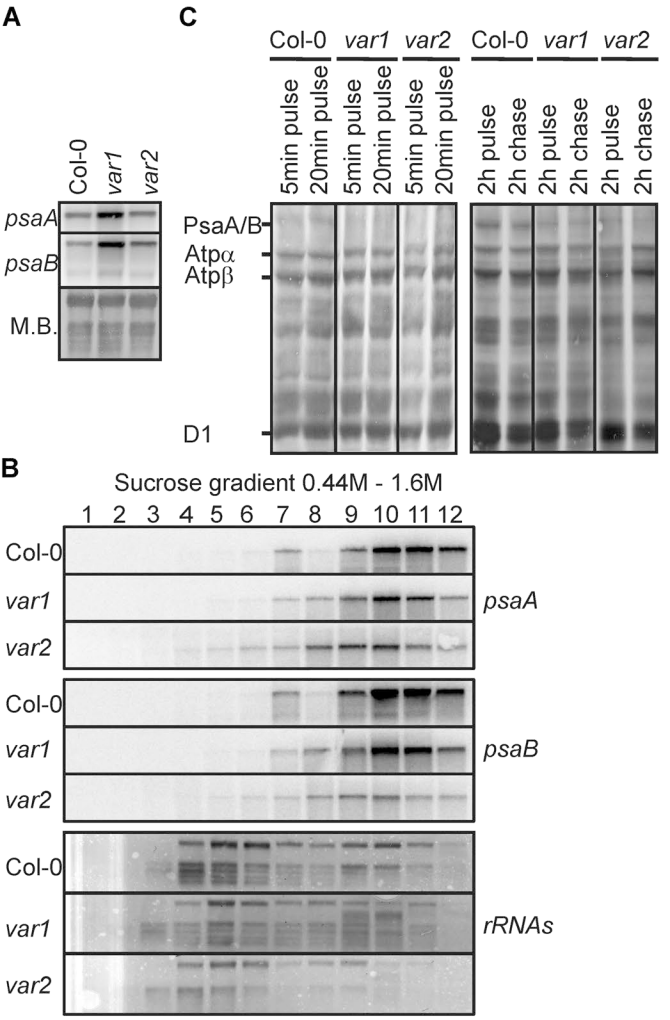

Figure 4. Biogenesis and degradation of PsaA/B in *var1*, *var2* and wild-type plants. A. Northern blot analysis of mRNAs encoding PSI core proteins. B. Association of mRNAs encoding PSI core proteins with polysomes. Polysomes were fractionated using ultracentifugation, mRNAs were separated by agarose gel electrophoresis and specific probes were used to indentify mRNA. C. *In vivo* pulse labeling. Leaves were pulse labeled under moderate light for five min and 20 min (left panel) or for two hours followed by two hours chase in the presence of unlabeled methionine (right panel). [^{35}S] methionine labeled proteins were separated by SDS-PAGE. Synthesis and degradation of the PsaA/B proteins was followed using autoradiogram films. A representative example from three independent biological replications is shown. Col-0, wild type. M.B. methylene blue.

Figure 5

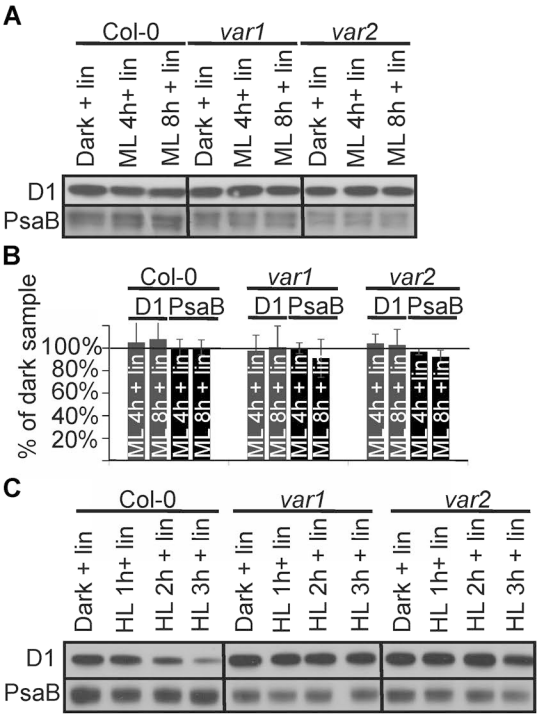

Figure 5. Degradation of D1 and PsaB proteins in the lincomycin treated *var1*, *var2* and wild-type leaves. 1mM lincomycin (lin) was incorporated into detached leaves trough petioles overnight in darkness. Leaves floating on water were shifted from darkness to A. and B. moderate light (ML, 120 µmol photons $m^{-2}s^{-1}$) or C. high light (HL, 800 µmol photons $m^{-2}s^{-1}$) prior thylakoid isolation and immunoblot analysis. B. Relative amounts of the D1 and PsaB proteins in wild type, *var1* and *var2* after the light treatments of leaves (as indicated in the figure B) and expressed as a proportion of respective dark controls (error bars indicate SD). Gels were loaded on equal chl basis. Col-0, Columbia-0.

Figure 6

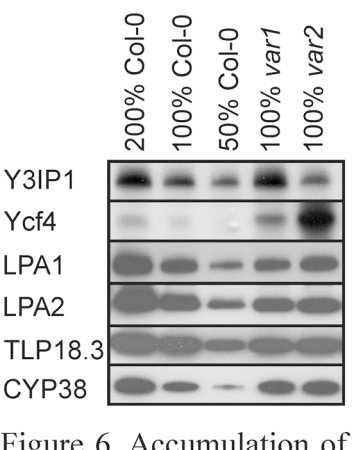

Figure 6. Accumulation of PSI and PSII auxiliary proteins in the *var1*, *var2* and wild-type plants. Immunoblots of the thylakoid membrane proteins separated by SDS-PAGE. Gels were loaded on chl basis. A representative example from three independent biological replications is shown. Col-0, wild type.

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