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Original Research Article

Direct Transcriptional Control of the Chloroplast Genes *psbA* and *psaAB* Adjusts Photosynthesis to Light Energy Distribution in Plants

Thomas Pfannschmidt,[1,2] Anders Nilsson, Anna Tullberg, Gerhard Link,[1] and John F. Allen

Plant Cell Biology, Lund University, Box 7007, S-220 07 Lund, Sweden
[1]Plant Cell Physiology and Molecular Biology, University of Bochum, Universitätsstr. 150, 44780 Bochum, Germany

Summary

Two photosystems, I and II, absorb and convert light energy in photosynthesis in chloroplasts of green plants. The genes *psbA* and *psaAB* of the cytoplasmic chloroplast genome encode core components of photosystem II and photosystem I, respectively. Here we show that the absolute amounts of photosystem I and photosystem II respond, in a complementary manner, to changes in light quality that preferentially excite each photosystem in mustard seedlings. We also show that the initial response to altered energy distribution is a change in the rates of transcription of *psbA* and *psaAB*. Changes in chlorophyll fluorescence emission in vivo suggest that the signal initiating this change is the oxidation–reduction state of plastoquinone, a component of the photosynthetic electron transport chain that connects photosystem I and photosystem II. The results are consistent with transcriptional effects observed previously with chloroplasts isolated in vitro and demonstrate that redox control of chloroplast transcription initiates long-term adjustments that compensate for imbalance in energy distribution and adapt the whole plant to altered light environments.

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INTRODUCTION

Light quality influences photosynthetic electron transport in higher plants, algae, and cyanobacteria. Changes in light quality, as they occur, for example, in the canopy of a forest or in aquatic environments, cause selective excitation of photosystem I (PS I)[3] or photosystem II (PS II) and thus produce an imbalance in energy distribution between the two photosystems. As a short-term response, such an imbalance is counteracted by so-called state transitions, in which the sizes of the light-harvesting antenna pigment complexes of PS I and PS II are posttranslationally controlled. As a long-term response, light quality also induces adjustments of photosystem stoichiometry, which have similar, but longer-lasting, functional effects (*1*, *2*).

Experimentally, photosystem stoichiometry adjustment in higher plant chloroplasts can be induced by growing plants in light sources favoring excitation of either PS I or PS II (*3*). Expression of genes coding for components of the two photosystems is affected in plants grown under such light sources (*4*, *5*) and is thought to be controlled at a posttranscriptional level (*5*). The molecular events leading to reversible photosystem stoichiometry adjustment (*6*) are unresolved, and it is not known whether the adjustment is produced by changes in the absolute amounts of PS I (*4*, *7*) or PS II (*8*).

Here we describe short-term and long-term responses of mustard seedlings grown under different and changing light qualities and report effects on the absolute quantities of the photosystem reaction centres, per plastid, of both PS I and PS II. In addition, we observed gene-specific responses to PS I- or PS II-light in the transcriptional rates of the corresponding photosynthesis genes, *psaAB* (encoding the reaction centre apoproteins of PS I) and *psbA* (encoding the D1 protein of PS II). Our data suggest a predominantly transcriptional control of *psaAB* gene expression during photosystem stoichiometry adjustment, whereas the

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Address correspondence to John F. Allen. Fax: 46-46-222-4009. E-mail: john.allen@plantcell.lu.se.

[2]Present address: Institute of General Botany, Department of Plant Physiology, University of Jena, Dornburger Str. 159, 07743 Jena, Germany.

[3]Abbreviations: P_{700}, reaction center chlorophyll of PSI; PS, photosystem (I or II); Q_A, plastoquinone Q_A.

expression of the *psbA* gene may involve both transcriptional and posttranscriptional events.

EXPERIMENTAL PROCEDURES

Plant Growth and Isolation of Chloroplasts and Chloroplast Subfractions. Mustard seedlings (*Sinapis alba* L.) were grown as described earlier (*9*). Mustard cotyledons were harvested 4 h after the beginning of the light period, and chloroplasts and thylakoid membranes were prepared by a method based on that of Walker (*10*). Chloroplast concentration was determined by counting the number of chloroplasts per unit volume of suspension with a hemocytometer. The same plastid suspension was used both for run-on transcription experiments and for isolation of thylakoid membranes used in spectroscopic measurements.

Spectroscopic Analyses. The chlorophyll content of thylakoid suspensions was determined spectroscopically and adjusted to 100 μM chlorophyll. P_{700} and plastoquinone Q_A (Q_A) concentrations were determined, with a Glynn Research single-beam spectrophotometer, as light-induced absorption change at 700 and 320 nm, respectively (*11*). Absorptivities (ε) used were 11 mM^{-1} cm^{-1} for Q_A (*12*) and 64 mM^{-1} cm^{-1} for P_{700} (*13*). Total chlorophyll concentrations were determined spectroscopically after extraction of cotyledons, chloroplasts, and thylakoids in 80% (v/v) buffered acetone (*14*). Concentrations of chlorophyll *a* and *b* were calculated by using the absorptivities reported by Porra et al. (*15*).

Cloned DNA Material. DNA probes representing mustard chloroplast genes were blotted onto nylon membranes for detection of labeled transcripts in run-on transcription experiments. PSA224-EBH1.9 was an internal *psaAB* probe, pSA364-E2.6 an *atpA* probe, and pSA120-E2.7 a *petA* probe (*16*). PSA204-EH1.0 was used as an internal *rbcL* probe and pSA452a as a *psbA* probe (*17*). PSA452-PS250 contains a 250-bp fragment of the *rpl2* intron cloned into pSPT18 and was used as a probe for *rpl2*. Other probes used were PSPTXX680, which contains *rps16* sequences (*18*); pBSE996, which spans the *trnG* 5′- and 3′-exon, including the complete intron sequences (*19*); pBSH895, which spans the 5′ portion of the *rrn16* gene; and pBSEX630, which is an internal portion of the *rpoB* gene (*20*). Clones used for in vitro synthesis of RNA probes labeled with [^{32}P]UTP were as follows: pBS-EH1.9, which contains the 1.9-kb fragment of pSA224-EBH1.9 cloned into pBluescript (Stratagene) (*psaAB* probe); pSA452a (*psbA* probe); and pBSEH633AT (*Tub-1* probe) (*21*).

Chlorophyll Fluorescence Measurements. Chlorophyll fluorescence was measured in vivo at 22 °C with a Hansatech modulated fluorescence measurement system. The cotyledons of a mustard seedling were fixed and illuminated with a modulated light-emitting diode light source (850 Hz) at 645 nm. Relative fluorescence intensity was measured at 700 nm with a modulated photodiode sensor, and the signal was amplified with a lock-in amplifier. State 1–state 2 transitions (*2*) were induced by switching between continuous PS I light and PS II light in the growth chamber. PS I light was provided by tungsten filament incandescent lamps shielded by a red, 650-nm cutoff filter. PS II light was provided by fluorescent strip lamps shielded by an orange broad-band filter with maximal transmittance at 560 nm.

Analysis of Chloroplast Gene Expression. Run-on assays were performed as described (*22*). Total incorporation of [^{32}P]UTP into transcripts was determined by precipitation with trichloroacetic acid (*23*). Gene-specific hybridisation signals were quantified after exposure of blots to phosphorimager screens. For northern analyses, total RNA from mustard cotyledons was prepared as described earlier (*24*). Electrophoretic separation, transfer of nucleic acids to nitrocellulose membranes, hybridisation with ^{32}P-labeled RNA probes, and washing steps were carried out by using standard protocols (*23*). Hybridization signals were detected by using X-ray film and phosphorimager screens for signal quantification.

RESULTS

Fig. 1A shows the intensity of modulated chlorophyll fluorescence of mustard (*S. alba* L.) seedlings that had been germinated and grown under either PS I light (PS I plants) or PS II light (PS II plants). Fluorescence then responded to PS I and PS II light in the way expected from previous studies of short-term adaptation, which is known to be caused by reduction and oxidation of plastoquinone (*2*). PS I→ II and PS II→ I plants showed a chlorophyll fluorescence signal resembling that of PS II and PS I plants, respectively, indicating an adaptational adjustment of photosystem stoichiometry in response to the change in the illumination condition. However, small differences in the kinetics and intensities of the fluorescence traces between either PS I→ II and PS II plants or PS II→ I and PS I plants (Fig. 1A) indicate differences in the organisation of the photosynthetic apparatus.

Selective illumination of PS I or PS II in chlorophyll *b*–containing plants and algae also produced changes in photosystem stoichiometry and thus in the chlorophyll *a*/*b* ratio (*8*, *25*). Fig. 1B shows that the initial chlorophyll *a*/*b* ratio of PS I plants and PS II plants is similar. If the seedlings were left in the growth light, no changes in chlorophyll *a*/*b* ratio occurred (results not shown). However, on changing the illumination of PS II light–grown seedlings to PS I light (PS II→ I plants), the chlorophyll *a*/*b* ratio decreased progressively, whereas changing the illumination of PS I light–grown seedlings to PS II light (PS I→ II plants) caused a chlorophyll *a*/*b* increase. The change in each direction had a half time of ~12 h, indicating a long-term, developmental response, and appeared to be complete 48 h after the change in light quality.

We determined the absolute extent of long-term adaptations by spectroscopic measurement of total quantities of both chlorophyll and photosystem reaction centre components Q_A (PS II) and P_{700} (PS I) on a per plastid basis. This revealed changes in the number of both PS I and PS II reaction centres (Table 1). Plants grown under a constant light regime showed small changes in comparison with white-light–grown control plants. PS I→ II plants and PS II→ I plants showed an adaptational response

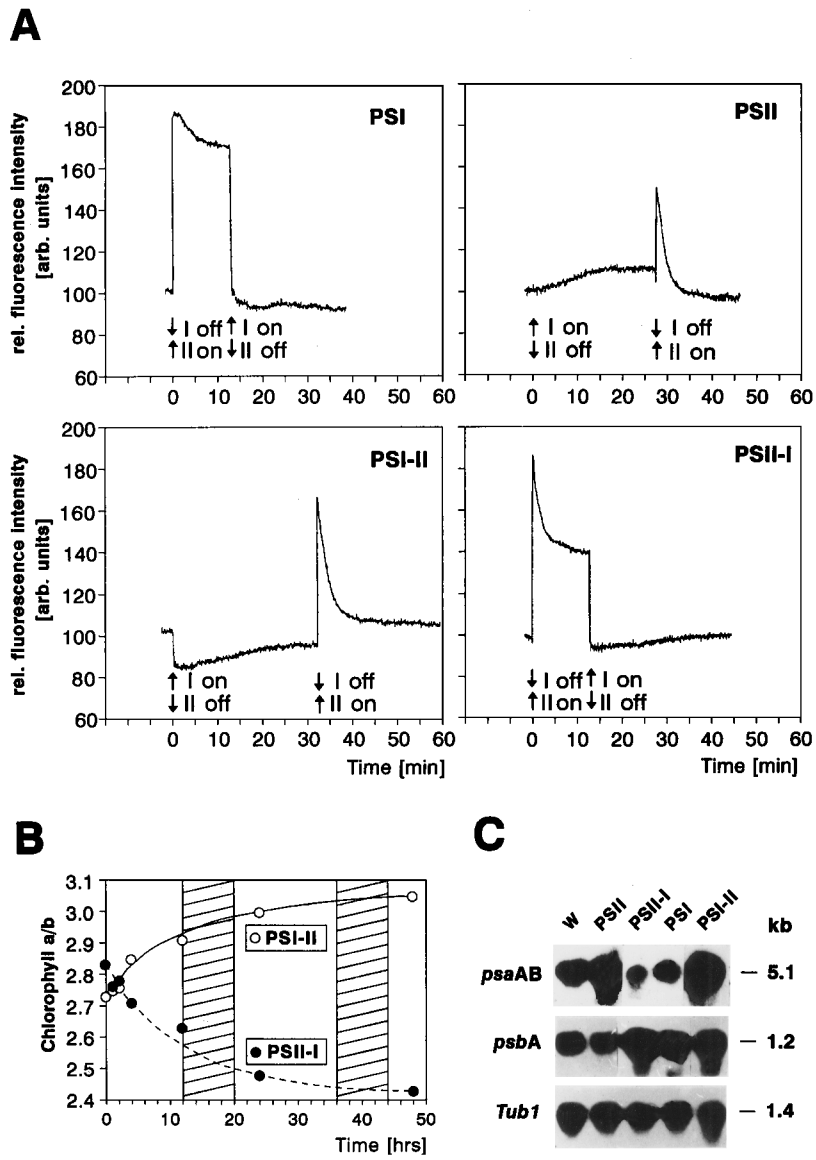

Figure 1. (A) Chlorophyll fluorescence emission at 700 nm obtained by weak, modulated excitation at 580–600 nm of mustard seedlings grown for 7 days under continous PS I or PS II light or grown for 5 days in PS I or PS II light followed by additional 2 days in the other light regime, as indicated in the upper right corner of each trace (PS I, PS II, PSI–II, and PSII–I). State 1–state 2 transitions were induced by switching between continuous PS I light and PS II light in the growth chamber (I on, II off, and vice versa). (B) Kinetics of changes in the chlorophyll *a/b* ratio of mustard seedlings in response to a switch between PS I and PS II light. Plants were grown 5 days from germination in light favoring either PS I or PS II. Each growth light regime was then replaced by the other (time point 0) and the chlorophyll *a/b* ratio was measured at intervals for 48 h (PSI-II and PSII-I). The hatched areas indicate the time of the constant dark period of 8 h. (C) Transcript amounts of *psaAB* and *psbA* genes in mustard seedlings grown under the same light regimes as in Tables 1 and 2. Loaded on each lane of the gel was 10 μg of total RNA. Samples were electrophoresed and blotted, and specific transcripts were detected after hybridization and autoradiography. Transcripts of the nuclear gene β-1 tubulin (*Tub1*) are shown as a control. Growth light conditions of seedlings used for RNA preparation are shown at top. Transcript sizes (kilobases) are given in the right margin.

Table 1

Absolute quantities of chlorophylls (Chl) and cofactors of integral protein complexes of thylakoid membranes in chloroplasts of mustard seedlings grown under three light regimes (white, PS II, PS I) and after the transfer between PS II- and PS I-specific lights (Q_A is the primary quinone electron acceptor of PS II; P_{700} is the reaction centre chlorophyll *a* of PS I)

Light source	Chl[a,b] [nmol]	Q_A[a] [pmol]	P_{700}[a] [pmol]
White	1.12	13.7 ± 2.0	7.1 ± 0.4
PS II	1.27	11.3 ± 2.3	8.3 ± 0.4
PS II → I	1.10	23.3 ± 2.0	6.2 ± 1.5
PS I	0.96	15.3 ± 1.9	6.6 ± 0.3
PS I → II	1.13	13.8 ± 2.1	12.4 ± 4.3

[a] Values are molar quantities in 10^6 plastids.
[b] Values represent means from three independent experiments. Variations of the given values were as much as ±0.05.

with much larger changes in reaction centre number. The total amount of chlorophyll, however, remained nearly constant.

We determined transcriptional rates for several plastid genes by performing plastid run-on transcriptional assays with chloroplasts isolated from plants grown under the different light conditions described above. As judged by incorporation of radioactive UTP into acid-precipitable material, overall transcriptional activity of chloroplasts from the various plants did not show major changes (data not shown). However, there were marked and highly significant gene-specific effects whose contributions to total RNA synthesis tended to cancel each other out. In Table 2, genes for photosynthesis-related proteins *psaAB*, *psbA*, and *rbcL* showed large changes in transcriptional rate in response to light quality. PS II light (constant or given for 48 h after 5 days of PS I light) increased the *psaAB* transcriptional rate in comparison with that in white light, whereas PS I light (constant or given for 48 h after 5 days of PS II light) decreased it. The opposite effect was observed in the case of *psbA*: here, PS I light increased the transcriptional rate in comparison with the control. This effect became even more apparent in the PS II → PS I plants, whereas the PS II light source produced no significant effect. The transcriptional rate changes of the *rbcL* gene in response to light quality exhibited the same pattern as that for *psbA*, but to a smaller extent. Table 2 also shows that rates of transcription of *petA*, *trnG*, and *rpoB* were independent of illumination conditions, whereas those of *atpA*, *rps16* and *rp12* were so low that any changes were below the limit of detection.

In northern analyses (Fig. 1C) we determined the transcript amounts of *psaAB* and *psbA*, the genes mainly affected in their transcriptional rate during photosystem stoichiometry adjustment. The transcript pool sizes of both genes exhibited the changes in the same direction as those found for their respective transcriptional rates.

Table 2

Transcriptional rates of nine different chloroplast genes under three light regimes (white, PS II, PS I) and after the transfer between PS II- and PS I-specific lights

	Light condition of plant growth				
Gene	White	PSII	PSII-I	PSI	PSI-II
psaAB	80 ± 11	163 ± 22	48 ± 12	57 ± 10	206 ± 17
psbA	452 ± 83	489 ± 75	767 ± 53	548 ± 78	498 ± 68
petA	41 ± 8	51 ± 6	52 ± 7	50 ± 10	53 ± 13
atpA	3 ± 4	6 ± 7	7 ± 7	12 ± 11	12 ± 7
rbcL	143 ± 19	188 ± 16	245 ± 35	224 ± 15	170 ± 25
rps16	3 ± 4	6 ± 4	7 ± 4	2 ± 3	12 ± 5
rpl2	8 ± 5	18 ± 7	13 ± 5	14 ± 1	14 ± 7
trnG	41 ± 13	36 ± 11	46 ± 8	51 ± 3	53 ± 17
rpoB	23 ± 2	20 ± 9	17 ± 4	27 ± 4	23 ± 3

Rates are expressed as values normalised to the respective signal of *rrn16*, which was set arbitrarily as 100%, and represent means from four or five independent experiments.

DISCUSSION

The photosynthetic apparatus in mustard cotyledons responds to light quality with short-term (Fig. 1A) and long-term adaptations (Fig. 1B and Table 1), as previously observed in other plants (*3*), but we also conclude that the photosystem reaction center adjustment results from complementary changes in the absolute number of both PS I and PS II reaction centres (Table 1). In all cases, a switch between light regimes during growth of the seedlings produces a stronger adaptational response than that which occurs under constant light quality. We conclude that a switch between light regimes induces a sudden change in energy distribution between the two photosystems, forcing a greater long-term response than that resulting from growth under constant illumination. Only the genes *psaAB*, *psbA* (encoding reaction centre proteins), and, to a smaller extent, *rbcL* show significant changes in response to light quality, indicating the operation of gene-specific regulatory mechanisms (Table 2). Comparison of the relative changes in RNA synthesis, transcript pool size, and number of photosynthetic reaction centers (Table 3) suggests that control of P_{700} apoprotein expression under these experimental conditions is exerted predominantly at the level of transcription. Transcriptional control of *psaAB* gene expression has previously been suggested in barley (*22*).

Effects of light quality on Q_A (Table 1) suggest large changes of *psbA* transcript pool size, whereas those on *psbA* transcriptional rate (Table 2) and PS II reaction centre accumulation (Table 3) occur in the same direction but take place to a smaller extent. This suggests the involvement of both transcript stability and transcriptional rate in changes in PS II reaction center number. *psbA* transcripts, in contrast to *psaAB* transcripts, are selectively stabilised during leaf development in barley (*26*, *27*).

Table 3
Light quality-induced changes in photosynthetic gene expression and reaction centre accumulation in relation to the respective values of white light control plants

	psaAB		PSI centre	*psbA*		PSII centre
Light source	Rate[a]	Amount[b]	number	Rate[a]	Amount[b]	number
PS II	+75.7%	+21%	+11.7%	+8.2%	−17%	−17.6%
PS II→ I	−39.5%	−67.1%	−13.1%	+69.7%	+123%	+70.7%
PS I	−29.2%	−33.9%	−7.2%	+21.3%	+83%	+11.9%
PS I→ II	+155%	+90.7%	+75.9%	+10.2%	+31%	+0.9%

[a] Transcriptional rate.
[b] Transcript amount.

Chlorophyll fluorescence measurements in vivo (Fig. 1A) point to the plastoquinone pool as the site of redox control of transcription that responds to changes in energy distribution between PS I and PS II, as suggested by previous findings for isolated chloroplasts (*9*). Transduction of this redox signal from the thylakoid membrane into different levels of control of chloroplast gene expression could be mediated by the redox-sensitive plastid transcription kinase (*28*, *29*) or by the redox-sensitive plastid RNA maturation enzyme p54 (*30*). These factors may be equivalent to the response regulators suggested in a previous model of transcriptional redox control (*31*, *32*).

We conclude that PS stoichiometry adjustment in higher plants is regulated by plastoquinone redox control of expression of chloroplast genes for the core proteins of the two photosystems. Redox control of *psbA* translational initiation may also contribute to the increase of PS II centre numbers under PS I light (*33*, *34*). Our data provide evidence for a new mechanism for the way in which photosynthesis adapts to changing environmental conditions by means of a fast and efficient feedback mechanism.

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