Light quality regulates expression of chloroplast genes and assembly of photosynthetic membrane complexes

(photosynthesis/thylakoid membrane/reaction center/DNA transcription/chloroplast adaptation)

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Communicated by Daniel I. Arnon, February 10, 1986

ABSTRACT The concentrations of photosystem I (PSI) and photosystem II (PSII) reaction centers and the level of chloroplast reaction center gene transcripts were determined in pea plants grown under different light-quality regimes. In plants grown in light primarily absorbed by PSI (“red” light), the PSII/PSI reaction center ratio was 2-fold greater than that in plants grown in PSII-sensitizing (“yellow”) light. In addition, the ratio of a PSI gene (psaA) transcript to a PSII gene (psaA) transcript was 2.6 times greater in red-grown plants relative to yellow-grown plants. Thus, a differential reaction-center concentration in the thylakoid membrane was accompanied by a differential expression of reaction center genes, suggesting that the synthesis of chloroplast membrane complexes and the assembly of photosystems are regulated by light quality at the transcriptional and/or post-transcriptional level.

The adaptability of higher plant chloroplasts to different environmental light conditions allows higher plants to succeed in a variety of habitats (1–7). It has been proposed that mechanisms of chloroplast adaptation involve both synthetic and degradative processes that modulate the relative concentration of specific chloroplast membrane complexes (8). In particular, the concentrations of photosystem II (PSII) and photosystem I (PSI) complexes vary in response to plant growth in different light-quality regimes (9, 10). Our work has explored in detail the light-quality regimes that cause an imbalance in light absorption between PSII and PSI and a subsequent imbalance in electron flow between the two photosystems. The response of the plant was a structural reorganization of the components of the thylakoid membrane such that the chloroplasts optimized the utilization of light prevailing in their environment. For example, chloroplasts from plants grown in PSII-sensitizing light were enriched in PSI complexes, while plants grown with light preferentially absorbed by PSI were enriched in PSII complexes (9, 10).

This is distinguished from the response elicited by variation in the photon flux density that causes changes in the light-harvesting chlorophyll (Chl) antenna size of PSII and PSI (2, 4–6) and in the concentration of the electron-transfer intermediates plastoquinone (PQ) and cytochromes b6 and f (Cyt b6/f) that function between PSII and PSI (1, 8).

To investigate the role of biosynthetic processes in chloroplast adaptation, we analyzed the expression of genes that code for polypeptides of PSII and PSI in plants grown under different light qualities. In the experiments reported here, the concentrations of PSII and PSI reaction centers were determined and compared to levels of transcripts of PSII and PSI reaction-center genes. The results indicate that mRNAs for photosynthetic reaction-center polypeptides accumulate to different levels, which are determined by yellow and red light regimes.

MATERIALS AND METHODS

Growth of Plants. Pisum sativum L. cv. Alaska was grown in the laboratory at 22°C under continuous illumination, which was provided either by 30-W General Electric cool-white fluorescent lights in combination with yellow Plexiglas (Rohm and Haas, no. 2208) or by 50-W incandescent bulbs filtered through red Plexiglas (Rohm and Haas, no. 2423) (Fig. 1). The energy fluence rate in the visible region was 34 microeinsteins (μE/m²·s⁻¹) and 14 μE·m⁻²·s⁻¹ for the yellow and red light, respectively. In spite of the difference in the two light intensities, the integrated absorbance of light by the chloroplasts was about the same under such yellow- and red-light conditions. The illumination used was selected to maximize differences in reaction-center concentrations. A light-intensity effect on reaction-center concentrations is not significant. As evidenced in previous work (3, 8), an 8-fold difference in light intensity during growth of Phaseolus vulgaris and Atriplex triangularis resulted in a 12–14% change in the PSII/PSI reaction-center ratio.

Isolation of Chloroplasts. Chloroplasts were isolated from 11-day-old seedlings as described (10). Chl concentrations and Chl a/Chl b ratios were determined in 80% (vol/vol) acetone extracts as described by Arnon (11).

Spectroscopic Measurements. Chloroplast absorbance-difference measurements were taken with a laboratory-constructed difference spectrophotometer (12). The concentrations of PSII and PSI were determined from quantitative measurements of Q, the primary quinone acceptor of PSII, and of P700, the reaction center of PSI, as previously described (13). The concentration of P700 was determined from the absorbance difference at 263 nm as described by McCauley and Melis (14). The concentration of Cyt f was measured with an Amino DW-2a spectrophotometer operated in the split-beam mode from the reduced-minus-oxidized difference spectrum of Cyt f. The reaction mixture contained 100–200 μM Chl, 2% (vol/vol) Triton X-100, and 0.33 mM K3Fe(CN)6. After registration of the baseline, hydroquinone was added to the sample cuvette to a final concentration of 2 mM. An equal volume of buffer was added to the reference cuvette. The optical path length of the cuvette was 1.0 cm, and a differential extinction coefficient of 18 mM⁻¹·cm⁻¹ was applied to quantitate Cyt f. The variation of the measurement of the photosynthetic electron-transport complexes was about 10%.

Isolation of Nucleic Acids. RNA was isolated from pea leaf tissue by grinding 5.0 g (fresh weight) of leaves with a mortar and pestle cooled by liquid N2. The powdered tissue was suspended in 25 ml of 50 mM Tris-HCl, pH 8.0/0.35 M

Abbreviations: PS, photosystem; Chl, chlorophyll; Q, primary quinone acceptor of PSII; P700, reaction center of PSI; PQ, plastoquinone; Cyt, cytochrome; μE, microeinsteins; kb, kilobase(s); SSC, standard saline citrate (0.15 M NaCl/0.015 M sodium citrate); rDNA, RNA-encoding DNA.

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sorbitol/25 mM EDTA/15 mM 2-mercaptoethanol/10 mM dithiothreitol/25 mM aurin tricarboxylic acid. The homogenate was filtered through two layers of Miracloth (Calbiochem), and cells were lysed by the addition of 2.5 ml of 5% (wt/vol) sodium sarcosinate/50 mM Tris-HCl, pH 8.0/25 mM EDTA. The lysed suspension was extracted with an equal volume of 50 mM Tris-HCl (pH 7.6)-saturated phenol, followed by extraction with an equal volume of phenol/chloroform/isoamyl alcohol, 25:25:1 (vol/vol) at 15°C. After centrifugation at 10,000 × g for 10 min, the aqueous phase was collected and precipitated with 0.5 M ammonium acetate and 2 vol of ice-cold ethanol (NH₄OAc/ EtOH) at −70°C for 1 hr. After centrifugation at 24,000 × g for 10 min at 4°C, the pellet was suspended in 10 mM Tris-HCl, pH 7.5/1 mM EDTA (Tris/EDTA). High molecular weight RNA was precipitated with 2 M LiCl overnight at 4°C. The RNA was collected by centrifugation at 24,000 × g for 15 min at 4°C, suspended in sterile H₂O, and stored at −20°C.

DNA was isolated from 2.5 g (fresh weight) of leaf tissue by using a procedure similar to the RNA isolation except that the powdered leaf material was suspended in a buffer without aurin tricarboxylic acid and the homogenate was not filtered through Miracloth. After the precipitation with ice-cold NH₄OAc/EtOH at −70°C for 1 hr and centrifugation at 24,000 × g for 15 min at 4°C, the pellet was suspended in Tris/EDTA and incubated with 10 μg of RNase A per ml at 37°C for 1 hr. After extraction with phenol/chloroform/isoamyl alcohol, the DNA was precipitated twice with ice-cold NH₄OAc/ EtOH, suspended in Tris/EDTA, and stored at 4°C.

Electrophoresis and Blotting of Nucleic Acids. RNA was denatured in 2.2 M formaldehyde/50% (vol/vol) formamide, incubated at 55°C for 15 min, and fractionated on a 1% agarose gel containing 20 mM morpholinepropanesulfonic acid (pH 7.0), 5 mM NaOAc, 0.5 mM EDTA, and 2.2 M formaldehyde (15). Electrophoresis was performed at 4°C. EcoRI/HindIII-digested DNA was incubated at 65°C for 5 min and fractionated on a 1% agarose gel in 89 mM Tris/89 mM H₂BO₃/2 mM EDTA, pH 8.3. After electrophoresis, the DNA was denatured by washing the gel with 0.5 M NaOH/1.5 M NaCl for 1 hr and was neutralized with 0.5 M Tris-HCl, pH 8.0/1.5 M NaCl for 1 hr. The RNA and DNA were blotted (Schleicher & Schuell, BA-85, 0.45 μm) as described by Thomas (16). The nitrocellulose filters were air-dried and baked in a vacuum oven at 80°C for 2 hr.

Gene Probes. Plasmid pSoc1080 is an 8.2-kilobase (kb) Pst I fragment of spinach chloroplast DNA inserted into pBR322 (E. Orozco, personal communication). The fragment contains the entire psaA gene. pSoc910 is a 12.3-kb Sal I spinach chloroplast DNA fragment inserted into pBR322 (E. Orozco, personal communication). It contains the genes psaA, psbC, and psbD. The probe used in the experiments reported here used a 9.0-kb Pst I/Sal I subfragment of pSoc910 that contained only psbC and psbD. The psbB probe is an oligonucleotide that consists of the first 50 nucleotides of the protein coding region of the spinach psbB gene. pH2A is derived from plasmid pHA1 and contains an 8.7-kb HindIII fragment of pea nuclear DNA inserted into pBR322 that contains the genes for 18S and 25S rRNA (17). pTCB8 is a 10.2-kb BamHI fragment of tobacco chloroplast DNA inserted into pBR322 and contains the coding sequences for 4.5S, 5.5S, 16S, and 23S rRNA and for tRNAAla and tRNAlnu (K. Shinozaki, personal communication).

Hybridization of Probes to RNA and DNA Blots. Nitrocellulose filters were prehybridized in 4× standard saline citrate (1× SSC is 0.15 M NaCl/0.15 M sodium citrate) and 1× Denhardt’s solution (18) for 3 hr at 68°C and then hybridized in 6× SSC/0.5% NaDodSO₄/1× Denhardt’s solution. The DNA probes were either nick-translated (Bethesda Research Laboratories nick-translation reagent kit) with [α-32P]ATP (p Soc1080, p Soc910, pH2A, and pTCB8) or 5’-end-labeled with [γ-32P]ATP using T4 polynucleotide kinase (psbB) as described in ref. 19. Double-stranded DNA probes were denatured, cooled, and added to the hybridization mixture. The blots were hybridized for 16–20 hr at 68°C. After hybridization the blots were washed with three changes of 2× SSC, followed by three changes of 1× SSC, for 20 min each, at 68°C. For hybridization with the psbB probe, the blots were prehybridized and hybridized in 6× SSC/20% (vol/vol) formamide/0.1% NaDodSO₄ containing 100 μg of yeast tRNA per ml at 42°C. After hybridization, the blots were washed twice with 0.18 M NaCl/10 mM NaH₂PO₄/1 mM EDTA, pH 7.4 (1× SSPE), and once with 0.1× SSPE. The filters were exposed to x-ray film at −70°C using intensifying screens. Autoradiograms of exposures in a linear range were scanned with a Joyce–Loebl microdensitometer and the relative intensity of a given band was determined by integration of the area under the peak. The autoradiograms shown are the results of representative experiments of repeated hybridizations. The variation of the measurement of RNA hybridization was + 20%.

RNA Dot-Blot Hybridization. Different amounts of RNA in a final volume of 20 μl were incubated at 75°C for 10 min, cooled, mixed with 120 μl of 20× SSC, and dotted onto distilled H₂O-washed nitrocellulose with a dot-blot manifold. Each spot was washed twice with 200 μl of 20× SSC. The filters were dried and baked for 2 hr at 80°C in a vacuum oven. The conditions for hybridization were the same as those used for the RNA gel blots.

RESULTS

Concentrations of Reaction Centers and Electron Transport Components. The illumination conditions used to grow the plants for the experiments reported here were chosen to produce a light quality that approximates the average excitation of one photosystem over the other. To determine the response of the photosynthetic apparatus to the resulting imbalance in electron flow between the two photosystems, we compared the concentrations of membrane complexes and the levels of expression of genes coding for photosynthetic proteins in PSI and PSII.

The concentrations of components of the photosynthetic apparatus varied as a function of growing pea plants in yellow or red light. The Chl a/Chl b ratio of the chloroplasts (3.0 in yellow and 2.5 in red; Table 1) indicated differences in the distribution of Chl-containing complexes (10). Quantitative measurements of Q and P₉₀₀ revealed significant differences in the concentrations of PSII and PSII complexes in the chloroplasts of plants grown under the two light qualities. The concentration of Q was greater in red-grown plants.
Table 1. Concentrations of Q (PSII) and P\textsubscript{700} (PSI) and of intermediate photosynthetic electron-transport components in pea plants grown under yellow or red light

<table>
<thead>
<tr>
<th></th>
<th>Chl a</th>
<th>Chl b</th>
<th>Q</th>
<th>PQ</th>
<th>Cytf</th>
<th>P\textsubscript{700}</th>
<th>P\textsubscript{90}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellow</td>
<td>3.0</td>
<td>571</td>
<td>188</td>
<td>1288</td>
<td>578</td>
<td>1.01</td>
<td></td>
</tr>
<tr>
<td>Red</td>
<td>2.5</td>
<td>496</td>
<td>122</td>
<td>1000</td>
<td>966</td>
<td>1.95</td>
<td></td>
</tr>
</tbody>
</table>

The concentrations of Q, PQ, and P\textsubscript{700} were determined from their respective light-induced absorbance changes at 320 nm (13), 263 nm (14), and 700 nm (13). The concentration of Cytf was determined from the reduced-minus-oxidized difference spectrum at 554 nm.

(Chl/Q = 496 in red versus 571 in yellow; Table 1). On the other hand, there was a substantial enrichment of P\textsubscript{700} in plants grown under yellow light (Chl/P\textsubscript{700} = 966 in red versus 578 in yellow; Table 1). The stoichiometry of PSII/PSI reaction centers (Q/P\textsubscript{700}) is thus different by a factor of about 2 in these plants. The adaptation of the photosynthetic apparatus to light quality is manifested predominantly in the modification of the chloroplast reaction center ratio. The concentration of components that function between PSII and PSI in electron transport (PQ and Cytf; see Table 1) is low, reflecting the low photon flux density under which both yellow-light and red-light plants were grown. Under growth conditions with higher photon flux density, there are higher relative concentrations of both PQ and Cytf (1).

Plants grown in light sensitizing mainly PSII contain more PSI. Conversely, plants exposed to PSII-sensitizing light contain more PSII. The plants thus respond to the prevailing light quality by synthesizing new complexes such that the relative concentrations of PSII and PSI in the chloroplast minimize the imbalance in light absorption by the photosystems.

Transcript Levels in Plants Grown Under Yellow or Red Light. The above results suggest that mechanisms exist in the chloroplast that regulate the relative amounts of PSII and PSI complexes in the thylakoid membrane. The mechanism underlying the response to light quality could involve the regulation of the expression of genes that code for proteins of the photosynthetic apparatus (8). To evaluate the role of gene expression in this process, the levels of mRNA of known chloroplast genes for PSI and PSII polypeptides were examined. Total RNA was extracted from plants grown in yellow or red light as well as from dark-grown (etiolated) plants. The amounts of RNA applied to the gels in all of the following experiments were standardized on quantitation of the fluorescence intensity of ethidium bromide-stained gels. In addition, the amounts of RNA applied to the dot blots were standardized on quantitation from the absorbance of the solution at 260 nm (see below). The RNA was size-fractionated, blotted to nitrocellulose, and hybridized with \textsuperscript{32}P-labeled gene probes. The RNA blot hybridization in Fig. 2A shows the transcript levels for cytoplasmic and chloroplast rRNAs in plants grown under yellow and red light and dark-grown plants. Cytoplasmic rRNA represents >80% of the total cellular RNA and does not change significantly (<5%) in plants grown under different light environments. It is convenient, therefore, to normalize the levels of chloroplast RNA in yellow, red, and dark-grown plants to the rRNA level. This procedure was applied routinely in our measurements to ensure a more precise RNA quantitation. The RNA blot in Fig. 2A shows that the levels of cytoplasmic rRNA (25S and 18S) loaded are similar for the yellow (lanes Y) and red (lanes R) samples. However, the levels of chloroplast rRNA transcripts (23S and 16S) are 45% greater in the yellow-grown plants relative to the red-grown plants and 10-fold greater relative to the etiolated plants (Fig. 2; see also Table 2). The complex pattern of chloroplast rRNA trans...
psbD is not well characterized but it has been proposed that the corresponding polypeptide is associated with PSII (26, 27) and it has been referred to as the “D2” (26, 28, 29) or the “32-kDa-like” (22) protein. The probe containing psbC and psbD hybridizes to six RNA species ranging in size from 2.0 to 4.5 kb (Fig. 3). The presence of two genes on the probe and the possible co-transcription of those genes (22, 23) makes identification of specific transcripts difficult but, in general, the levels of these chloroplast transcripts were greater in yellow-light-grown plants relative to red light-grown plants (Table 2). The RNA dot-blot hybridizations (Fig. 3B) support our contention that quantitative differences exist in the levels of the PSI and PSII reaction center gene transcripts in the plants grown with different light qualities.

There are several RNA species that hybridize to the psbB probe, which is specific for the “51-kDa” Chl a protein of PSII (Fig. 4). The strongest hybridization was to a 2.2-kb transcript and the level of this transcript was 5- to 10-fold greater in yellow- and red-light-grown plants relative to dark-grown plants (Table 2). The levels of the other transcripts were not significantly different among yellow- and red-light-grown and etiolated plants.

A similar pattern of transcripts was detected in RNA blots of spinach RNA (30). Probes specific for the gene for the “51-kDa” Chl a apoprotein of the PSII reaction center (psbB) as well as the genes for Cyt b6 (petB) and subunit 4 (petD) of the Cyt b6-f complex hybridized to RNAs of similar molecular weight, suggesting that these genes are transcribed as a polycistronic message in spinach (30, 31). The similarity of the psbB hybridization pattern for pea RNA shown in Fig. 4 (left lanes) with the pattern observed in spinach suggests that an analogous transcriptional organization exists in pea.

The likelihood that psbB is part of a polycistronic transcription unit and the variability in the levels of the transcripts hybridizing to the psbB probe are indicative of differential stability of the individual mRNAs that constitute the polycistronic message. In particular, the increase in the level of the 2.2-kb transcript in light-grown plants relative to that of etiolated plants as well as the accumulation of the 2.2-kb transcript to different levels in the red- and yellow-green plants suggest that accumulation of the 2.2-kb message is both light-stimulated and affected by light quality.

The nitrocellulose filter that was used with the psbB probe was also used for other hybridization experiments. The psbB probe was washed from the filter with 5 mM Tris-HCl, pH 8.0/0.2 mM EDTA/0.5% sodium pyrophosphate/1X Denhardt’s solution for 1 hr at 65°C (16). Complete removal of the probe was tested by exposing the washed filter to x-ray film. This filter was subsequently hybridized with psaA, exposed to x-ray film, and then hybridized with the chloroplast rDNA probe as an internal control (Fig. 4, right lanes). The psaA probe was not removed before hybridizing the filter with the rDNA probe and so the large psaA transcript as well as the 23S and 16S rRNA transcripts are seen in the autoradiogram. Comparison of the results obtained using three different probes with the same filter clearly shows that steady-state chloroplast gene transcript levels are different in plants grown under different qualities of light. Transcript levels were quantified from densitometric scans of the autoradiograms. The ratio of PSII/PSI gene transcripts (psbB/psaA versus psbC/psbD/psaA) was 2.2 to 2.6 times greater in red-grown plants than in yellow-grown plants (Table 2), establishing a correlation between steady-state transcript levels and the levels of PSII and PSI complexes in the chloroplast.

The observed differences in transcript levels cannot be attributed to changes in DNA content that may have been a result of plant growth in red or yellow light. Hybridization of Southern blots of restriction-digested DNA showed that there was no significant difference in (psaA) gene dosage in plants grown under yellow or red light (Fig. 5).

**DISCUSSION**

The effect of light quality on the organization of the photosynthetic apparatus is manifested primarily in the modulation of the relative PSII and PSI complex concentration. Differences in the stoichiometry of PSI and PSII complexes among yellow- and red-light-grown plants were paralleled by differences in the steady-state level of chloroplast gene transcripts coding for PSI and PSII polypeptides. Thus, in pea plants grown under yellow light, the relative concentrations of transcripts encoded by the genes psaA (apoprotein of P700), psbB (51-kDa protein of PSII), and psbC/psbD (44-kDa

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**Table 2. Levels of chloroplast gene transcripts in pea plants grown under yellow or red light**

<table>
<thead>
<tr>
<th>Chloroplast rRNA*</th>
<th>psaA</th>
<th>psbC/psbD</th>
<th>psbB†</th>
</tr>
</thead>
<tbody>
<tr>
<td>psbB/psaA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dark 100</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Yellow 1040</td>
<td>145</td>
<td>440</td>
<td>935</td>
</tr>
<tr>
<td>Red 715</td>
<td>30</td>
<td>195</td>
<td>500</td>
</tr>
</tbody>
</table>

Transcript levels were quantified from densitometric scans of autoradiograms exposed within the linear range of the x-ray film. The densitometer traces were measured on lighter exposures of the autoradiograms shown in Figs. 3 and 4. Variability in the intensity of hybridization signals with different probes occurs because of differences in the length of the chloroplast gene probes and because the psbB probe is labeled only at the 5′ end while the other probes were labeled by nick-translation.

*All transcripts.
†The 2.2-kb transcript.
‡Arbitrarily set equal to 1.0.

**Fig. 4. Hybridization of nick-translated psaA (specific activity, 9.5 x 10⁶ cpm/μg of DNA) and chloroplast rDNA (specific activity, 2.5 x 10⁶ cpm/μg of DNA) probes and psbB oligonucleotide (specific activity, 1.4 x 10⁶ cpm/μg of DNA) to RNA blots of pea leaf RNA from plants grown under yellow (lanes Y) or red (lanes R) light and from dark-grown (lanes D) plants. The lanes marked “E. coli” contain RNA isolated from *Escherichia coli*, which was included as a control and as a molecular weight marker. The autoradiograms were exposed for 42 hr. Other conditions were as in Fig. 2.**
protein/32-kDa-like protein of PSII) paralleled the relative concentrations of their respective proteins in the thylakoid membrane. We conclude that molecular mechanisms must exist that regulate the levels to which chloroplast gene transcripts accumulate.

Given the significant changes of $P_{1990}$ mRNA levels under yellow or red light, it is possible that regulation of $psaA$ expression occurs at the transcriptional level. In this case, it would appear that yellow light promotes whereas red light inhibits the transcription of $psaA$ (Fig. 3). The analysis of promoter regions for other genes has indicated that variability in promoter strengths and/or regulatory components could be responsible for differential transcription of chloroplast genes (32, 33). Moreover, differences in $psaA$ expression could also be a consequence of differential stability of the 6.3-kb transcript. This would affect the entire transcript, since no processing or processing products have been observed for the different light treatments in this study or for the spinach transcript (21). The results of the hybridization with the $psbB$ probe also suggest that the mature $psbB$ transcript accumulates to different levels in the dark versus in yellow or red light, although there is no significant difference in the amount of polycistronic primary transcript in these plants (Fig. 4). Moreover, work with etiolated spinach seedlings showed that in the dark petB and petD mRNAs (coding for Cyt b6 and subunit 4 of the Cyt b$_6$f complex, respectively) accumulate, but $psbB$ mRNA does not (34).

These results imply that regulation of $psbB$ expression may occur exclusively at the post-transcriptional level. A complete answer to this question would require careful comparison of plastid mRNA levels and their half-lives that currently are not available.

The molecular mechanism by which light-quality signals are identified by the chloroplast and the process by which they are transmitted at the DNA level is presently unknown. The possibility of a phycotochrome-mediated modulation of gene transcription under different light qualities cannot be entirely excluded although a substantially different activation of phycotochrome in yellow- and red-light-grown peas seems unlikely. This contention is based on the observation that both the yellow and the red light source used in this work emitted light of sufficient intensity at 660 nm to effect phycotochrome activation (Fig. 1). Recently, it was proposed that imbalanced electron flow between PSI and PSII initiates the transmission of a "signal" that ultimately causes changes in both synthetic and degradative metabolic processes in the plant (8). The results presented in this report establish a correlation between imbalanced electron flow (induced by light quality) and gene expression (i.e., transcription and/or post-transcriptional events) that are involved in synthesis of chloroplast proteins. This system could serve as a model to guide future experiments.

R.E.G. was supported by a postdoctoral fellowship from the McKnight Foundation. The work was supported in part by the Shell Development Co. (contract M552 to W.G.) and by a U.S. Department of Agriculture Competitive Research Grant to A.M. We thank Dr. E. M. Orozco for providing the $psaA$, $psbC$/$psbD$ probes, Dr. M. Sugiuara and Dr. K. Shinozaki for the chloroplast DNA probe, Dr. W. F. Thompson for the cytoplasmic rDNA probe, and Dr. G. Zurawski for the oligonucleotide probe. We also thank Dr. Birgit Piechulla and Dr. Jonathan Narita for helpful suggestions during the course of this investigation.