Plant Physiol. (1985) 79, 371-376
0032-0889/85/79/0371/06/$01.00/0

Phytochrome Control of Levels of mRNA Complementary to Plastid and Nuclear Genes of Maize[1]

Received for publication December 26, 1984 and in revised form June 3, 1985

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ABSTRACT

The involvement of phytochrome in the control of the levels of RNA transcribed from maize plastid and nuclear genes was examined. The effects of illumination with red light, far-red light, or red light followed by far-red light on relative amounts of RNAs complementary to maize plastid genes for the large subunit of ribulose bisphosphate carboxylase (RuBPCase); the 32-kilodalton thylakoid membrane triazine herbicide binding B protein of photosystem II; the α, β, and ϵ subunits of CF_1; subunit III (proton-translocating) of CF_0; the reaction center proteins A1 and A2 of photosystem I; two other light-induced genes for membrane proteins of photosystem II (ORFs 353 and 473); and one gene for an unidentified membrane protein (UORF 443) were measured by hybridization of labeled DNA probes to samples of leaf RNA. Transcripts of two nuclear-encoded genes, the genes for the small subunit of RuBPCase and the light-harvesting chlorophyll *a/b* binding protein, were studied in the same way. The levels of RNA complementary to all of these light-induced genes were significantly increased within 3 to 6 hours after brief illumination with red light. The stimulatory effects of red light were largely reversed by subsequent illumination with far-red light. It is concluded that phytochrome controls increases in the levels of mRNAs complementary to certain plastid and nuclear genes in dark-grown maize seedlings.

During light-induced development of etioplasts into chloroplasts, morphological, structural and biochemical changes occur, including the accumulation of Chl, the formation of thylakoid membrane proteins and lipids, increases in levels of some enzymes, an increase in chloroplast RNA polymerase activity, and increases in various RNA species (1, 5, 6, 10, 14, 17, 25, 28). The first major plastid DNA sequence whose transcript level was shown to increase during greening was photogene 32, the gene for a 32-kD thylakoid membrane polypeptide in maize (3, 17). This polypeptide has been shown to bind triazine herbicides and appears to be the B protein of PSII; thus, the gene is designated *ps2B* (23). (It has also been designated *psbA* [18].) Photo-regulation of *ps2B* transcription has also been reported in other plants (12, 20, 28). Recently, a number of other photoregulated genes have been mapped on the maize chloroplast chromosome and characterized in this laboratory (8, 25; Castroveijo, K. M. T. Muskavitch, E. T. Krebbers, H. Roy, D. R. Russell, L. Bogorad, unpublished data). These include, in addition to *ps2B*: *rcL*—encoding the large subunit of ribulose biphosphate carboxylase (19); *cflA B* and *E*—encoding the α, β, and ϵ subunits, respectively of CF_1[4] (25; S. Rodermel, L. Bogorad, unpublished data) the coupling factor 1 for photosynthetic phosphorylation; *cfoIII*—encoding subunit III of CF_0 (25); *ps1A1* and *ps1A2*—encoding polypeptides of P700—the reaction center of PSI (13, 25); ORFs 473, 353—encoding PSII proteins of 473 and 353 amino acids, respectively—and UORF 443—encoding an unidentified membrane polypeptide (E. T. Krebbers, K. M. Muskavitch, E. A. Orr, R. Schantz, M. Castroveijo and L. Bogorad, unpublished data). In addition, expression of nuclear genes *rcS* (encoding the small subunit of ribulose biphosphate carboxylase) and/or *cab* (encoding the light harvesting Chl *a/b* binding protein) have been demonstrated to be induced by light in barley, *Lemna*, pea, bean, and maize (2, 16, 25, 28, 29). For convenience, the term 'photogene' is used to designate a gene whose transcript level increases significantly during light-induced development.

The major photomorphogenic system of plants is driven by the R and FR reversible phytochrome receptor (11, 21, 22, 27). In some cases, a blue light receptor may be involved in photomorphogenesis (21, 24). Phytochrome is a bile pigment-protein complex that has two photointerconvertible forms: Pr and Pfr with absorption maxima at 660 and 730 nm, respectively (11). Photoconversion of Pr to Pfr by R potentiates a diverse array of morphogenic responses that are not exhibited if the Pfr is promptly reconverted to Pr by illumination with FR.

To understand the molecular mechanisms that govern light-dependent changes during greening, it is necessary to identify the photoreceptor (or photoreceptors) that regulate expression of maize photogenes. It has been shown by others (2, 16, 20, 26, 28, 29) that RNA levels of *rcS*, *cab*, *ps2B*, and *rcL* are affected by phytochrome in at least one plant species. The results presented here demonstrate that the levels of RNAs complementary to these and several other sets of photoregulated plastid and nuclear genes of maize are controlled by phytochrome.

MATERIALS AND METHODS

Growth of Plants. Maize seeds (FR9 cms X FR 37; Illinois Foundation Seeds, Inc.) were soaked overnight in running water

[1] Various segments of this research were supported in part by research grants from the National Science Foundation, the Competitive Research Grants Office of the United States Department of Agriculture, and the National Institute of General Medical Sciences (L. B.). It was also aided by the Maria Moors Cabot Foundation for Botanical Research of Harvard University.

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[4] Abbreviations: CF_1, coupling factor for photosynthetic phosphorylation; cpDNA, plastid DNA; ORF, open reading frame; UORF, unidentified open reading frame; R, red light; FR, far-red light; kb, kilobases; kbp, kilobase pairs.

and sown in moist Vermiculite. Seedlings were grown in narrow plastic trays (36 × 7 × 5 cm) in the dark at 25°C for 8 to 10 d.

Light Treatment. Monochromatic light was obtained from Airequipt 125 500-W projectors equipped with Baird-Atomic interference filters. The R source had a peak transmittance at 660 nm and an energy fluence rate of 0.9 W/m^2 at the level of plants. For the 725 nm FR source, this value was 0.7 W/m^2.

Extraction of RNA. About 10 g of leaves were harvested from the seedlings under a dim green safe light and ground in a mortar with liquid N_2. The frozen powder was suspended in 25 ml of hot lysis buffer (0.2 M sodium borate, 30 mM EGTA, 2% (w/v) sodium triisopropylnaphthalenesulfonate, pH 9.0) and was extracted with phenol/chloroform by the procedure previously described (9). After repeated precipitation with alcohol and centrifugation, the RNA pellet was resuspended in 2 M LiCl. The final pellet was dissolved in distilled H_2O and analyzed spectrophotometrically and by agarose gel electrophoresis.

Isolation of Chloroplast and Plasmid DNA. cpDNA was prepared as described previously (9). Plasmid DNAs were isolated and purified by cesium chloride centrifugation. The designations of the cloned plasmids used for probing transcripts of plastid and nuclear genes of maize are listed in Table I together with the sizes of the cloned inserts and the genes encoded.

Radioactive Labeling of DNA. Plasmid DNA for hybridizations to membrane-bound RNA samples was labeled with (α-^{32}P) dATP by the nick-translation reaction. Labeled plasmid DNA was separated from unincorporated nucleotides by chromatography on Biogel P-60.

Dot Blots. Aliquots of RNA were denatured by heating to 60°C in 7.5% formaldehyde, 10 mM Na-phosphate (pH 6.8), for 30 min, according to the procedure of White and Bancroft (30). For analysis by hybridization with radioactive DNA probes, series of RNA containing dots were formed on strips of Gene Screen Hybridization Transfer membrane (New England Nuclear). Each 5-mm diameter dot was formed by applying 5 μg RNA in 10 μl to the Gene Screen Membrane presoaked in 2XSSC (1XSSC = 0.15M NaCl, 0.015 M Na-citrate) by gentle capillary action using a stack of four layers of wet 3 MM-Whatman paper and dry paper toweling (about 2 cm high) underneath the Gene Screen. Dot blots were air-dried and membranes were baked in a vacuum at 80°C for 4 h.

Northern Blots. Total leaf RNA was glyoxylated in 1 M glyoxal, 10 mM Na-phosphate (pH 6.8) at 50°C for 1 h and separated electrophoretically on 1.2% agarose gel using TBE (89 mM Tris, 89 mM boric acid, 2.5 mM EDTA, pH 8.3) as running buffer (9). The denatured RNA in 2XSSC was transferred to Gene Screen by blotting. These 'Northern' blots were dried and baked in the same manner as the Gene Screen dot blots.

Hybridization. Gene Screen sheets carrying RNA samples as dot blots and Northern blots were presoaked in hybridization buffer (50% [v/v] formamide, 3XSSC, 0.1% [w/v] SDS, 1X Denhardt's solution, 100 μg/ml calf thymus DNA) at 37°C for 4 h, then hybridized with nick-translated ^{32}P-labeled plasmid DNA (10^6–10^7 cpm) in 10 ml of fresh hybridization buffer at 42°C for 16 h (9). After hybridization, the Gene Screen membranes were washed extensively in 2XSSC, 0.5% (w/v) SDS, at 65°C for 1.5 h, then in 1XSSC, 0.1% SDS (w/v), at 65°C for another 1.5 h. In experiments using heterologous plasmid probes for *rcS* and *cab* from pea and barley respectively, less formamide (10%) and lower temperatures were used for hybridization (37°C) and washing (42°C) for better hybridization.

The washed and dried dot and Northern blots were exposed to x-ray films at −70°C using intensifying screens for autoradiography. To assess mRNA quantitatively in the dot hybridization, several exposures of the films were scanned with a Zeineh Soft Laser Scanning Densitometer with a peak area integrator. This allowed us to estimate the level of an individual mRNA relative to total RNA which is mainly rRNA. A linear relationship was found between the scanner readings and the RNA on the Gene Screen in amounts of 5 μg and below hybridized with ^{32}P-labeled DNA (about 10^6 cpm) for a strip of 10 RNA dots. Therefore, aliquots containing identical amounts of total RNA (5 μg), monitored both by spectrophotometry (*A* at 260 nm) and RNA gel electrophoresis (mainly cytoplasmic 25S, 18S rRNA, and plastid 16S, 23S rRNA) were spotted onto Gene Screen.

RESULTS

Increase in Maize Plastid Photogene RNAs under Continuous or Intermittent Illumination. The time courses of increases in the levels of RNAs complementary to photoregulated plastid genes in response to continuous or brief intermittent illumination were determined in the following experiment conducted to establish

Table I. *Plasmids Used for Probing Transcripts of Plastid and Nuclear Genes of Maize*

Gene Location	Plasmid	Insert	Size (bp)	Gene(s) Encoded[a] (19)	(18)	References
Plastid[b]	pZmc461	Pst-Pst (from Bam9)	560	*rcL*	*rbcL*	(19)
	pZmc427	BamHI-EcoRI (from Bam8)	2000	*ps2B*	*psbA*	(7), (25)
	pZmc545	Bam2	9800	ORFs353,473		[c] (19)
	pZmc527	Bam3	8700	*cf1A* *cf0III*	*atpA* *atpH*	(19), (25)
	pZmc415	Bam24	1450	*cf1A*	*atpA*	(19), (25)
	pZR4876	Sal (from Eco *e*)	2700	*cf1BE*	*atpBE*	(19)
	pZmc556	Bam17	2500	*ps1A1*		(13), (19), (25)
	pZmc404	Bam21′	1670	*ps1A2*		(13), (19), (25)
	pZmc569	Bam20	1700	UROF 443		[d] (19)
	pZmc518	Bam13, 17′	3100, 2500	*r16*	*16S rDNA*	(19)
Nucleus	pSSU160	HindIII (pea)	160	*rcS*		(4)
	pAB96	Pst (barley)	850	*cab*		(16)

[a] Two parallel nomenclatures given are presented in references 18 and 19. [b] Plastid probes were cloned maize plastid DNA sequences as designated by Larrinua *et al.* (19) and listed in the "Inserts" column. [c] E. T. Krebbers, K. M. T. Muskavitch, L. Bogorad, unpublished data. [d] R. Schantz, E. A. Orr, L. Bogorad, unpublished data.

conditions for illumination with monochromatic light. Eight d-old dark-grown maize plants were exposed to continuous white light; a single 1-min white light pulse ('1'); or two 1-min white light pulses separated by a 3-h interval of darkness ('2'). Plants were harvested 3, 6, or 9 h after initiation of illumination (Fig. 1, bottom right). The changes in the level of transcripts of *rcL*, *ps2B*, *ps1A1*, *ps1A2*, and maize plastid Bam fragment 3 containing cf1A and cfOIII were measured by dot hybridization and are shown as time-course curves in Figure 1. The results indicate that not only continuous white light but also a single white light pulse (1 min) is sufficient to bring about an increase in the level of RNAs complementary to various photoregulated genes that is detectable after 3 h of dark incubation following the light pulse. However, the levels of complementary RNAs under continuous light increased more than under light pulses, and two light pulses separated by 3 h induced higher levels of complementary RNAs than a single light pulse. Brief illumination with R resulted in similar kinetics for the appearance of RNAs (data not shown). A program of brief illumination, 3 h of darkness, brief illumination, and harvest after 3 h of additional darkness was used in subsequent experiments to study the involvement of phytochrome. This experimental sequence resulted in changes in RNA pool sizes that were adequate to measure while it reduced the probability of secondary effects that might occur when using continuous illumination or repeated brief illumination over periods of days rather than hours.

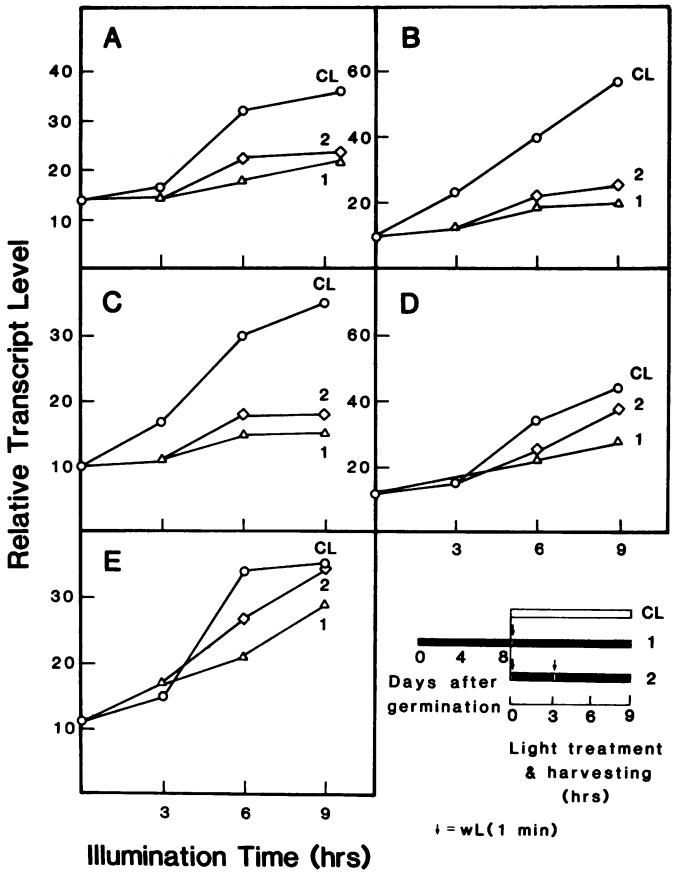

FIG. 1. Levels of maize photogene transcripts after illumination of etiolated seedlings with pulses of white light. Eight d-old dark-grown plants were treated with (line CL) continuous white light; one (line 1) or two (line 2) 1-min pulses of white light (WL) at 0 and 3 h as marked by arrows. The treatment program is shown in the diagram at the lower right-hand corner. Total RNA was isolated at 0, 3, 6, 9, h and hybridized with plasmid probes for *rcL* (A), *ps2B* (B), *cf1A*, and *cfOIII* included in plastid chromosome fragments Bam 3 (C), *p1A1* (D), and *ps1A2* (E). The transcript levels were measured by dot hybridization and expressed as scanning units. The numbers are the averages of three measurements for a given RNA. The variations in values were from 4 to 15% of the average.

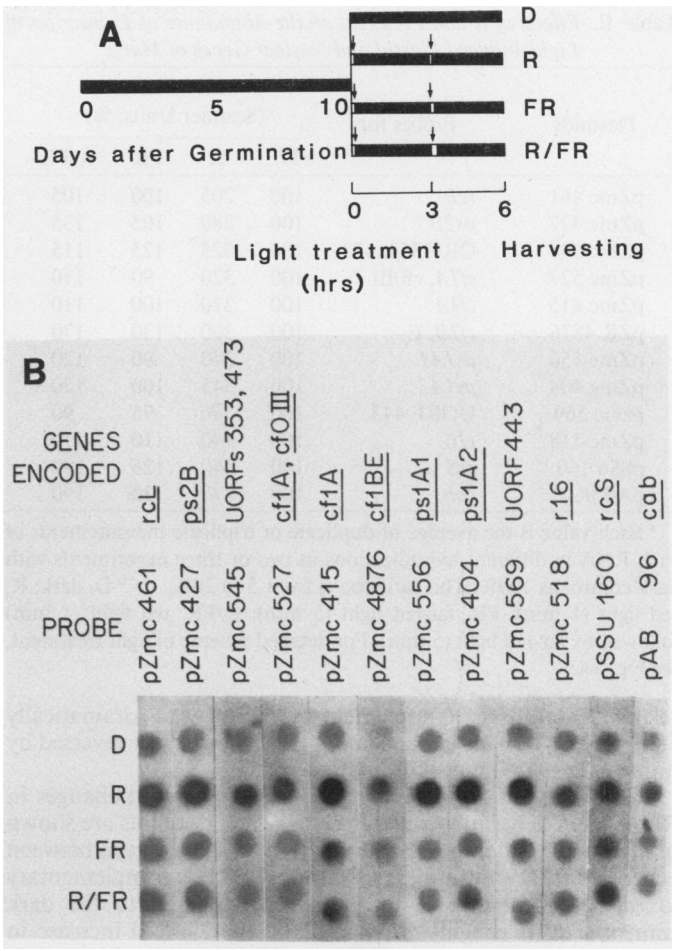

FIG. 2. A, Scheme of R and FR treatments. Maize plants were grown in the dark for 10 d, then illuminated with R (1 min), FR (5 min), or R/FR (1 min/5 min) at 0 and 3 h, as indicated by the arrows. The leaves were harvested at 6 h. Dark bars represent periods in darkness. B, Dot hybridization of maize RNA with cloned probes for plastid and nuclear genes. Total RNAs were extracted from dark-grown leaves or leaves illuminated with R, FR, or R/FR, as shown in A. Equal amounts of RNA (5 μg) were denatured and spotted onto Gene Screen, hybridized with ^{32}P-labeled probes, and exposed to x-ray film, as described in "Materials and Methods." The scanning densitometer values of films from similar experiments are shown in Table II.

Phytochrome Control of the Levels of Plastid and Nuclear Photogene RNAs. The involvement of phytochrome in controlling photogene expression was tested by briefly exposing etiolated maize plants to R (1 min) or to FR (5 min) or to R (1 min) followed by R (5 min) and measuring the relative levels of complementary RNA (Fig. 2A). Morphological changes in plants exposed to different light treatments were checked roughly to verify that the illumination conditions used elicited classical phytochrome-mediated responses in etiolated maize seedlings. After all the plants were moved to continuous white light for 24 h directly from darkness or exposed to two R pulses each followed by 3 h darkness, those seedlings preilluminated with R pulses showed, more rapid Chl accumulation than seedlings not preilluminated with R pulses.

Dot Blots. Figure 2B shows dot hybridization analyses of maize leaf mRNA from different light treatments using ^{32}P-labeled cloned probes. For each previously identified photogene, the

Table II. *Effects of R and FR Light on the Abundance of Transcripts of Light-Induced Plastid and Nuclear Genes of Maize*

Plasmids	Probes for	mRNA Levels (Scanner Units, %)[a]			
		D[b]	R	FR	R/FR
pZmc 461	*rcL*	100	205	100	105
pZmc 427	*ps2B*	100	280	105	135
pZmc 545	ORF 353, 473	100	325	125	115
pZmc 527	*cf1A*, cf0III	100	320	90	110
pZmc 415	*cf1A*	100	370	100	110
pZR 4876	*cf1B*, E	100	300	130	170
pZmc 556	*ps1A1*	100	340	90	120
pZmc 404	*ps1A2*	100	345	100	120
pzmc 569	UORF 443	100	340	95	90
pZmc 518	*r16*	100	140	110	110
pSSu 160	*rcS*	100	240	125	190
pAB 96	*cab*	100	270	130	190

[a] Each value is the average of duplicate or triplicate measurements of each RNA in different hybridizations in two or three experiments with dark control as 100%. The variation is from 5 to 20%. [b] D, dark; R, red light (1 min); FR, far-red light (5 min); R/FR, red light (1 min) followed by far-red light (5 min). For detailed scheme of light treatment, see Fig. 2A.

relative amounts of complementary RNAs were dramatically enhanced by R. This enhancement effect was largely reversed by immediate subsequent illumination with FR.

Table II lists the magnitudes of the light-induced changes in RNAs from experiments like that for which dot blots are shown in Figure 2B. Differences of about 10 to 20%, were seen between experiments. For example, the amount of RNA complementary to *rcL* doubled after R illumination compared to the dark control. This is roughly comparable to the 2.4-fold increase in RNA complementary to *rcS*. R-induced increases in RNA pools complementary to photogenes ranged up to about 3.5 to 3.8-fold. Exposure to FR alone generally had no effect; the increases of about 20% (UORFs 353, 473, and *rcS*) after illumination with FR are probably not significant. Illumination with FR for 5 min immediately following each 1-min exposure to R blocked the effect of R almost completely except for *ps2B*, *cf1BE*, *rcS*, and *cab*; in these cases, reversal was incomplete. The levels of maize plastid rRNAs exhibit a transitory increase of approximately 10 to 20% after about 3 h of continuous illumination of dark-grown seedlings (J. E. Davey, L. Bogorad, unpublished data); the slight apparent increase in transcripts of *r16* (the gene for 16S rRNA) here tends to confirm the earlier observation.

Northern Blots. Northern blot analyses were carried out for mRNAs of some photogenes; these confirmed the results of the dot blot assays. Equal amounts of total leaf RNA were separated electrophoretically by size on agarose gels. The denatured RNA transcripts were transferred to Gene Screen and hybridized with ^{32}P-labeled nick translated DNA probes for transcripts of *rcL*, *ps2B*, *r16*, *ps1A1*, and *ps1A2*. The results of autoradiography are shown in Figure 3. The major transcripts of *rcL* (1.6 plus 1.8 kb) and *ps2B* (1.2 kb) increased remarkably upon R irradiation. This increase was reversed if FR treatment followed exposure to R. The same is true for *ps1A1* and *ps1A2* whose major transcripts are 3.3 kb, 1.7 kb and 3.7 kb, 2.2 kb, 1.75 kb, respectively. However, *r16* showed a relatively stable transcript (1.54 kb) level after illumination with R.

DISCUSSION

The 139-kbp maize plastid chromosome is comprised of two large inverted repeats of 22 kbp each plus two unique regions. Thus, the chromosome contains 117 kbp of unique sequences (19). Photogenes occupy about 19% of the unique sequences and are distributed among at least six different transcription units (25; K. M. T. Muskavitch, E.T. Krebbers, L. Bogorad, unpublished data). These transcription units could not be distinguished by the kinetics of increase in complementary RNAs upon illumination of dark-grown plants but showed three distinctive patterns of change on prolonged continuous illumination (25). In this investigation, we have focused on the question of whether or not phytochrome is involved in regulating the initial increases of RNA levels for these maize photogenes upon illumination of dark-grown seedlings.

Many photoregulated developmental phenomena in plants are mediated by phytochrome. Although it is not clear yet exactly how and at which level it acts, Mohr (21) proposed that phytochrome might regulate "differential gene activation and gene repression." This hypothesis has been supported by the observations that the levels of RNA transcripts of *rcS*, *cab* (in barley, Lemna, pea and bean), *ps2B* (in mustard, pea and bean), and *rcL* (in pea and bean) are affected by phytochrome (2, 16, 20, 26, 28, 29). We have used somewhat different illumination procedures and come to the same conclusions for etiolated maize seedlings with regard to these as well as other genes.

We have shown here, by dot blot and Northern hybridization procedures, that increases in the levels of transcripts complementary to maize photogenes, *ps2B*, *rcL*, *ps1A1*, *cf1A*, *cfOIII*, and *cf1BE* as well as the photogenes UORF 443, ORF 353, and ORF 473 observed after illumination of dark-grown seedlings (25; K. M. T. Muskavitch, E. T. Krebbers, L. Bogorad, unpublished data) are regulated via phytochrome. The increases are observed after brief illumination with R but the effect of illumination by R is completely or largely reversed by FR, as is characteristic of phytochrome-mediated photomorphogenesis. However, the possibility of involvement of photoreceptors other than phytochrome cannot be ruled out; the synthesis of some plant proteins is responsive to blue light (24). Rodermel and Bogorad (25) have shown that, in continuously illuminated dark-grown seedlings, the levels of transcripts of several maize photogenes drop after reaching maxima after 10 to 20 h in the light. The results described in this paper do not address the mechanism responsible for these drops.

Many developmental and metabolic changes are triggered by illumination of etiolated seedlings. For example, some limited photosynthetic activity begins within a few minutes after commencement of illumination. The optimal experimental arrangement is to induce a change large enough to measure with confidence in the parameter under study while eliciting no, or only the smallest possible, changes in other, possibly interacting, systems. We have chosen experimental conditions close to the minimum needed to elicit clearly measurable changes in RNA pool sizes in order to minimize possible effects of secondary changes on RNA metabolism. Earlier work showed that illumination of etiolated maize seedlings with white light for 1 min initiated plastid maturation effects that were completed over a period of about 3 h in darkness, and could be reinforced by an additional brief exposure to light (14).

In the present experiments, we have measured only RNA pool sizes because of technical limitations that do not permit us to determine rates of transcription *in vivo*. The size of each pool reflects the sum of synthesis and destruction. It seems unlikely that changes in pool sizes observed here result from constant rates of synthesis of photogene RNAs coupled with photoinduced changes in RNA lifetimes without postulating rises and falls in the activities of a number of ribonucleases that act on specific transcripts. First, RNA pools for most maize plastid genes do not change significantly during light-induced development of etioplasts to chloroplasts (25). Second, transcripts of at least one region of the maize plastid chromosome decrease, rather than

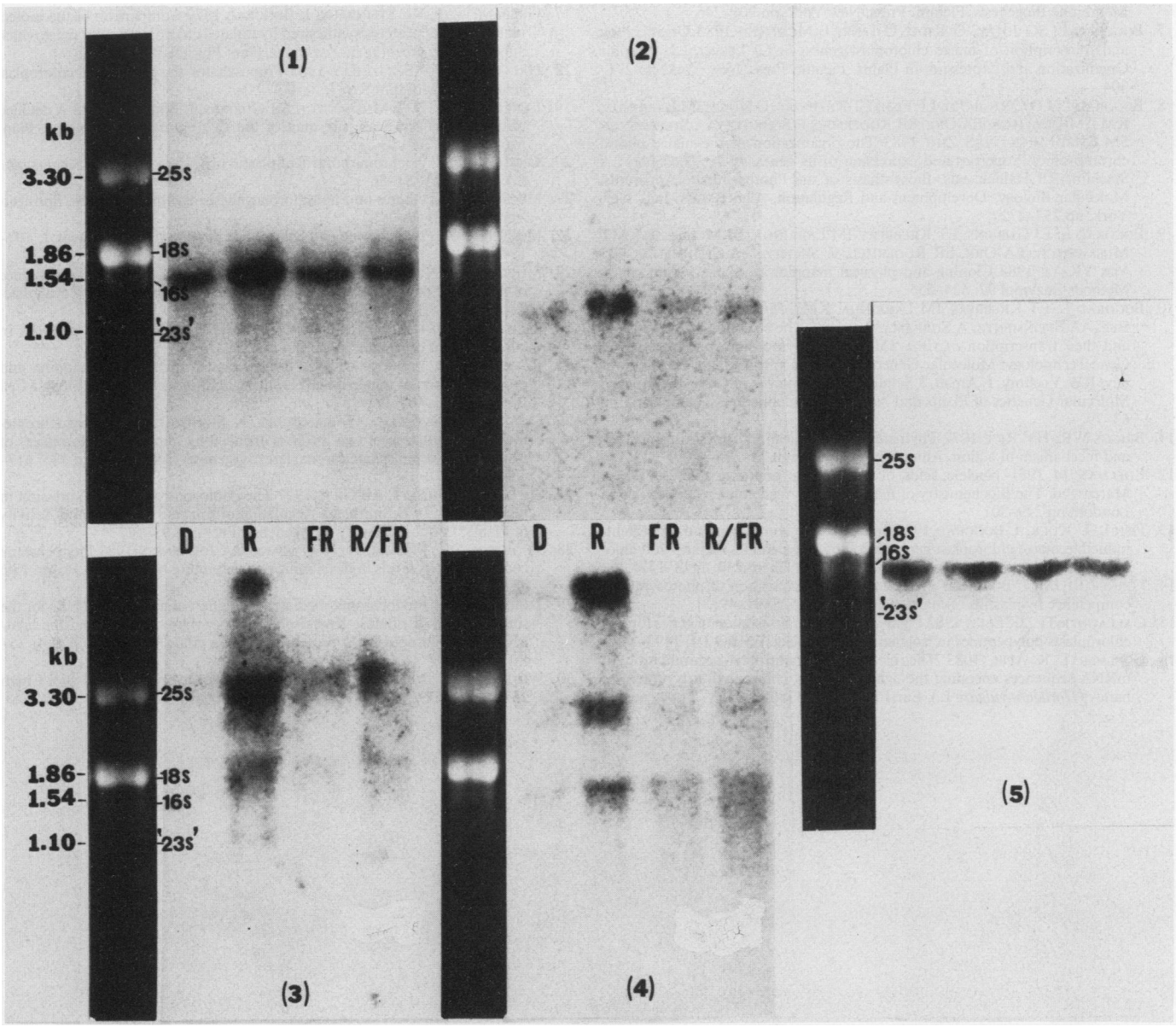

FIG. 3. Northern hybridization of maize RNA with cloned labeled probes for plastid genes. Equal aliquots (15 μg) of glyoxylated RNA from dark-grown (D) maize leaves or from leaves of plants subjected to treatment with R, FR, or R/FR were fractionated electrophoretically on 1.2% agarose gels, transferred to Gene Screen, and hybridized with ^{32}P-labeled probes (Table I) for *rcL* (1), *ps2B* (2), *ps1A1* (3), *ps1A2* (4), *r16* (5). Four treatments (DR, FR, R/FR) have the same patterns and same intensities of rRNA on the gels. The ethidium bromide-stained gels are shown in the left-hand panels corresponding to each probe. The locations of cytoplasmic 25S and 18S rRNAs, plastid 16S rRNA, and '23S' rRNA breakdown products which are used as mol wt markers are indicated on the gels. The sizes of RNAs are indicated by numerals (kb).

increase, in amount after illumination (J. Lukens, L. Bogorad, unpublished data). Thus, it seems most reasonable to conclude that phytochrome, acting somewhere in the cell, regulates one or more events leading to increases in the rates of transcription of maize plastid photogenes. This suggestion is also supported by Gallagher and Ellis's finding, using isolated nuclei from dark and light-grown pea leaves, that light increases the transcription of the genes *cab* and *rcs* (15).

Acknowledgments—We thank S. R. Rodermel for his technical help, and K. M. T. Muskavitch, L. Fish, and E. A. Orr for providing plasmids pZmc 545, pZmc 404, and pZR 4876, respectively. We also thank J. Bedbrook and K. Apel for providing plasmids pSSu 160 and pAB 96, respectively.

Note Added in Proof—UORF 353 has been shown to code for the D-2 protein of PS II and UORF 473 to be the gene for the 44 kD Chl protein of the PS II reaction center (E. T. Krebbers, K. M. T. Muskavitch, M. Castroveijo, H. Roy, D. R. Russell, L. Bogorad, unpublished data).

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