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Developmental regulation and phytochrome-mediated induction of mRNAs encoding a proline-rich protein, glycine-rich proteins, and hydroxyproline-rich glycoproteins in *Phaseolus vulgaris* L.

(bean/cell wall structural proteins/light regulation/organ specificity/photomorphogenesis)

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ABSTRACT **We have studied developmental and light regulation of mRNAs encoding a putative cell wall proline-rich protein (PvPRP1), cell wall glycine-rich proteins (GRPs), and cell wall hydroxyproline-rich glycoproteins (HRGPs) in bean (*Phaseolus vulgaris*). Light increases the levels of these mRNAs 2- to 150-fold in highly spatially regulated patterns during seedling development. These mRNA changes include differential regulation of transcripts derived from the GRP and HRGP multigene families. In 6-day-old light-grown seedlings, the PvPRP1 and GRP1.0 mRNAs were most abundant in the apical region of hypocotyls, epicotyls, and roots. In contrast, several HRGP transcripts were most abundant in the mature region of hypocotyls and roots in light-grown seedlings. When etiolated 6-day-old seedlings were illuminated with white light for 8 hr, maximal accumulation of PvPRP1 and GRP1.0 mRNAs occurred in the apical hook, whereas HRGP and GRP1.8 mRNAs accumulated in the mature region of hypocotyls. Etiolated seedlings subjected to a pulse of red light accumulated PvPRP1, GRP, and HRGP mRNAs in the hypocotyls. Far-red light inhibited red light induction of these mRNAs, indicating a phytochrome-mediated process. The possible roles of PRPs, GRPs, and HRGPs in cell differentiation and photomorphogenesis are discussed.**

The structure and composition of plant cell walls vary depending on cell type, developmental stage, and environmental conditions. Three classes of cell wall structural proteins have been best characterized (1, 2). In dicotyledonous plants, hydroxyproline-rich glycoproteins (HRGPs), also known as extensins, contain tandem repeats of Ser-Hyp_4 (3, 4). Glycine-rich proteins (GRPs) largely consist of repeating Gly-Xaa in which Xaa is frequently glycine (5, 6). Proline-rich proteins (PRPs) also possess repeating motifs and typically contain approximately equal levels of proline and hydroxyproline (7–10).

All three classes of cell wall proteins and their encoding mRNAs are expressed in specific organs and cell types (11–13). For example, three transcripts of the PRP gene family in soybean (SbPRP) are differentially localized in several cell types in stems, including vascular tissues, cortical cells, and the endodermoid layer (14). In addition, differential regulation by wounding, fungal elicitor, and infection has been described for mRNAs encoding all three classes of cell wall proteins in several species (6, 10, 15–17).

A wealth of information exists on whole plant and cellular photomorphogenesis and the underlying physiological and biochemical changes (18, 19). Since light has a profound effect on cell expansion and differentiation, it would be expected to be a major factor regulating cell wall structural protein gene expression. However, very limited information is available on light regulation of HRGP, GRP, and PRP gene expression. Wall-bound hydroxyproline in etiolated pea seedling epicotyls increased upon red light-stimulated conversion of the phytochrome photoreceptor to its physiologically active form (20). In etiolated tomato seedlings, phytochrome was shown to be involved in negative regulation of HRGP mRNA levels (G. Dechamp-Guillaume, D. Rumeau, and M. T. Esquerre-Tugaye, personal communication). Marcus and co-workers (21) found that SbPRP2 mRNA was reduced in the upper part of hypocotyls after exposure of 2-day-old etiolated soybean seedlings to white light.

In this paper, we show that light stimulates the accumulation of PRP, GRP, and HRGP transcripts in different regions of bean seedling shoots. In illuminated 6-day-old seedlings, highest levels of a PRP transcript (PvPRP1) and a GRP transcript (GRP1.0) were found in the apical region of hypocotyls and epicotyls. In contrast, HRGP transcripts and the GRP1.8 transcript predominate in the mature region of hypocotyls. All three classes of mRNAs were regulated by activation of phytochrome. Our findings suggest that the differential spatial accumulation of cell wall structural protein mRNAs is an important component in the process of photomorphogenesis.

MATERIALS AND METHODS

Plant Materials. Seeds of *Phaseolus vulgaris* cv. Tendergreen (Burpee) were surface sterilized, soaked in water overnight, and planted in vermiculite. Seedlings were grown at 25°C either in the dark or illuminated with white light [fluence rate, 450 $\mu E/m^2 \cdot sec$ (E, einstein; 1 E = 1 mol of photons); 11-hr dark/13-hr light cycles]. For red and far-red light treatments, the λ_{max} values were 665 nm for red light and 722 nm for far-red light (22). Fluence rates were as follows: red light, 8–12 $\mu E/m^2 \cdot sec$; far-red light, 15–20 $\mu E/m^2 \cdot sec$; white light, 60 $\mu E/m^2 \cdot sec$. Seedlings were grown for 6 days in darkness before light treatments. A dim green safe light was used in the manipulations. After dissection of plants, samples were immediately frozen in liquid nitrogen and stored at −70°C.

RNA Blot Hybridization. RNA isolation and blot hybridization were performed as described (23) with the following modifications: (*i*) 5 μg of total RNA per lane was loaded in all gels; (*ii*) nylon membranes (Zetaprobe, Bio-Rad) were used; (*iii*) final wash conditions were 40 mM sodium phosphate buffer (pH 7.2) containing 1% SDS at 65°C for the PvPRP1 probe and 60°C for the HRGP probe. Quantitative comparisons were based on densitometric scanning of the autoradiograms in the linear range of film exposure.

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Abbreviations: GRP, glycine-rich protein; HRGP, hydroxyproline-rich glycoprotein; PRP, proline-rich protein.

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DNA Probes and Labeling. The subcloned 527-bp fragment representing the 3′ half of the *PvPRP1* cDNA clone was isolated and ^{32}P labeled by the random primer method (23). The HRGP probe consists of equal amounts of labeled inserts from cDNA clones *Hyp3.6* and *Hyp4.1* (15).

RESULTS

Regulation of PvPRP1, HRGP, and GRP mRNAs in Dark- and Light-Grown Seedlings. We examined the levels of PvPRP1, HRGP, and GRP transcripts in 2-day-old dark- and light-grown plants by RNA blot hybridization. At this age, the dark- and light-grown seedlings were covered with vermiculite and were morphologically identical (Fig. 1*A*). Fig. 1*B* shows that PvPRP1 mRNA was very abundant in epicotyls of dark-grown seedlings. In addition, the mRNA is detected in radicles and cotyledons. Light-grown seedlings contained comparable levels of PvPRP1 mRNA in all regions relative to dark-grown seedlings with the exception of increased expression in section 2 of radicles. Equal loading of RNA on all blots used in this study was verified by equal intensities of ethidium staining of 28S and 18S rRNAs and hybridization with a cDNA clone complementary to an abundant, constitutive RNA, H1 (data not shown; ref. 23).

Fig. 1*C* shows that the HRGP probe hybridized to six transcripts. The 4.4- and 2.5-kb mRNAs are homologous to the *Hyp3.6* and *Hyp4.1* HRGP cDNA clones, respectively, used as the probe (15). The 7.0- and 3.3-kb mRNAs correspond to previously reported HRGP mRNAs (15, 16) and the 1.8- and 0.9-kb mRNAs correspond to GRP transcripts designated GRP1.8 and GRP1.0, respectively (6). Cross-hybridization of GRP transcripts is supported by several lines of evidence. First, a previous report showed that GRP1.8 double-stranded DNA probe (GGX-rich on one strand) cross-hybridized with the 4.4- and 2.5-kb HRGP mRNAs (CCX-rich) under hybridization conditions comparable to those we used (6). Second, double-stranded *Hyp3.6* and *Hyp4.1* DNA probes cross-hybridized to a 1.8-kb mRNA later identified as GRP1.8 (15). Third, we have shown that *Hyp4.1* and *Hyp3.6* probes hybridized to the expected size fragments on genomic Southern blots corresponding to HRGP and GRP genes described in previous studies (data not shown; refs. 6 and 15).

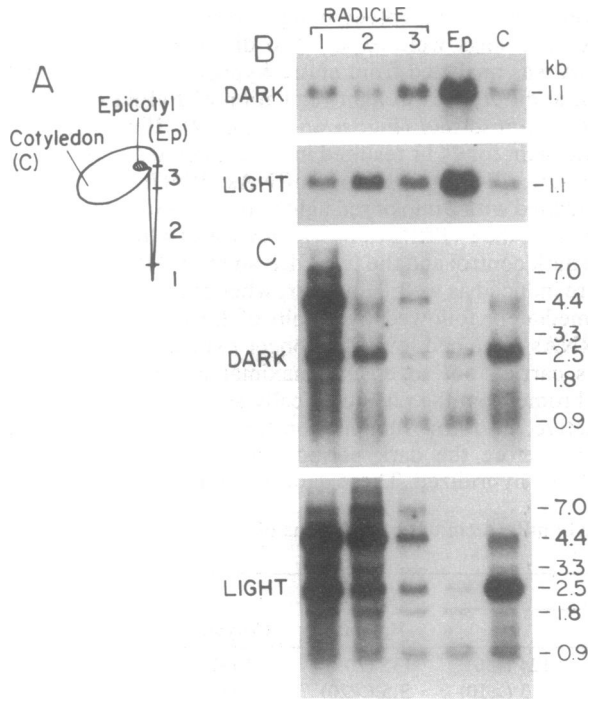

FIG. 1. Northern blot analysis of RNA from dark- and light-grown 2-day-old seedlings. (*A*) Samples were sectioned as illustrated. Radicles were sectioned as follows: 1, 5-mm section below the tip; 2, 5- to 10-mm section between 1 and 3; 3, 5-mm section below the cotyledon. C, cotyledon excluding seed coat; Ep, epicotyl. Blot was hybridized with the PvPRP1 probe (*B*) and rehybridized with the HRGP probe (*C*).

In contrast to the PvPRP1 mRNA, the overall levels of HRGP mRNAs in dark-grown seedlings were highest in section 1 of radicles and lowest in epicotyls. The 4.4- and 2.5-kb transcripts were the major hybridizing species in section 1, while the 2.5-kb transcript predominated in section 2 and cotyledons. In light-grown seedlings, several HRGP transcripts occurred at higher levels in radicles and cotyledons compared to the dark-grown counterparts. In addition, the GRP1.8 mRNA predominated in the radicle and was more abundant in the light, while the GRP1.0 mRNA was most abundant in the cotyledons of both sets of seedlings.

The expression of PvPRP1, HRGP, and GRP mRNAs was also examined in 3-day-old seedlings (data not shown). All three classes of mRNAs were elevated in roots compared to hypocotyls regardless of illumination. The light-grown seedling hypocotyls contained small but distinctly higher accumulations of the PvPRP1, GRP, and HRGP mRNAs compared to the dark-grown counterparts. In epicotyls, dark-grown seedlings had decreased, whereas light-grown seedlings had about the same PvPRP1 mRNA levels as the 2-day-old seedlings.

After 6 days of growth, dark-grown seedlings showed characteristic etiolated seedling morphology, while the light-grown counterparts exhibited shorter hypocotyls without hooks and epicotyl growth (Fig. 2*A*). Fig. 2*B* shows that the PvPRP1 mRNA was highest in the roots of etiolated seedlings compared to other organ parts. The hypocotyls contained little PvPRP1 mRNA, but a low level was detected in the mature region. By comparison, the PvPRP1 mRNA was more abundant in all organ parts of light-grown seedlings. The most dramatic difference between dark- and light-grown seedlings was the much higher level of PvPRP1 mRNA in the apical region of the latter. The PvPRP1 was maintained in epicotyls

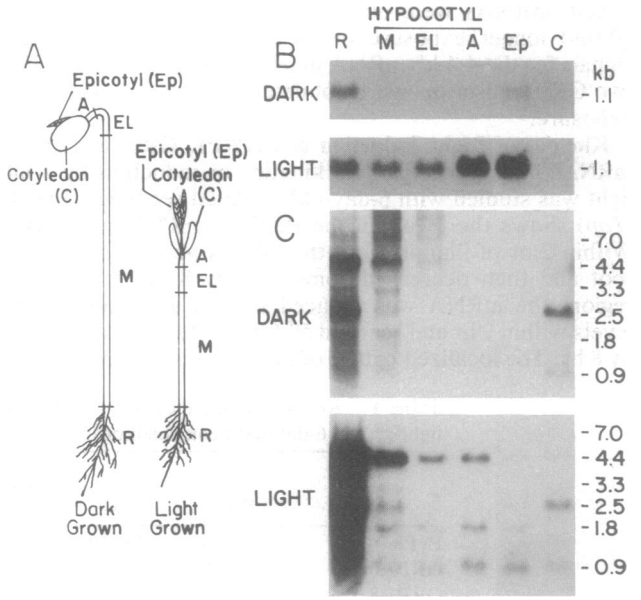

FIG. 2. PvPRP1, GRP, and HRGP mRNA levels in dark- and light-grown 6-day-old seedlings. (*A*) R, root (excluding the root–hypocotyl junction). Hypocotyls were sectioned as follows: M, mature; EL, 10-mm section just below A; A, apical 5-mm section below cotyledon. Blot was hybridized with the PvPRP1 probe (*B*) and rehybridized with the HRGP probe (*C*).

and cotyledons at levels comparable to those in 2-day-old seedling organs, while the mRNA continued to decrease in the etiolated 6-day-old counterparts. Table 1 provides a quantitative description of the RNA levels presented in Fig. 2.

The two GRP mRNAs were comparably regulated in etiolated seedlings but differed in their patterns of regulation in light-grown seedlings (Fig. 2*C* and Table 1). The two mRNAs were more abundant in all organ parts in light-grown compared to dark-grown seedlings except for cotyledons, which had comparable levels. The GRP1.0 mRNA distribution was very similar to that of the PvPRP1 mRNA, with highest levels in the apical hypocotyl region and epicotyls of light-grown seedling shoots. In contrast, the GRP1.8 mRNA level was elevated throughout the hypocotyl and low in epicotyls.

In etiolated seedlings, HRGP mRNA expression was generally similar to that of the PvPRP1 and GRP mRNAs (Fig. 2*C* and Table 1). While both 4.4- and 2.5-kb HRGP mRNAs were abundant in roots, the 4.4-kb mRNA predominated in hypocotyls. In light-grown seedling roots, the 4.4- and 2.5-kb mRNAs were present at higher levels than in the dark-grown counterparts. The light-grown seedling hypocotyls also contained higher levels of these two HRGP mRNAs, particularly in the mature region. Interestingly, the 7.0- and 3.3-kb HRGP mRNAs were present at reduced levels in light-grown seedling hypocotyls compared to etiolated counterparts.

In 8-day-old light-grown seedling hypocotyls and epicotyls, the levels of PvPRP1, GRP, and HRGP mRNAs were reduced compared to the levels in 6-day-old seedlings (data not shown). In addition, the predominant accumulation of PvPRP1 and GRP1.0 mRNAs in the apical hypocotyl was transient since these mRNAs were uniformly distributed in the 8-day-old seedling hypocotyls.

Expression of PvPRP1, GRP, and HRGP mRNAs in 3-Week-Old Plants. PvPRP1, GRP, and HRGP mRNA expression was also examined in later plant development. Fig. 3*B* shows that PvPRP1 mRNA was detectable in young leaves (L1) but not in older leaves (L2 and L3). As had been observed in 8-day-old seedling hypocotyls, the transcript was present throughout the stem at similar levels. In addition, the PvPRP1 mRNA was detectable in roots. The 4.4- and 2.5-kb HRGP mRNAs were observed only in roots (Fig. 3*C*). A 10-fold longer exposure of the same blot revealed weak signals for the 4.4-kb mRNA in leaves (data not shown). The two GRP transcripts were not detectable, even at the longer exposure.

Kinetics of Light Induction of PvPRP1, GRP, and HRGP mRNAs in Hypocotyls. The kinetics of induction by white light was studied with 6-day-old etiolated seedlings. Fig. 4*B* (*Top*) shows the levels of the PvPRP1 mRNA in the dark. Within 2 hr of illumination, the mRNA accumulated in the root and then decreased somewhat by 8 hr. In the hook region, the mRNA was induced from nearly undetectable levels within 2 hr and reached 50-fold higher than dark levels by 8 hr. The localized nature of induction is clearly shown in

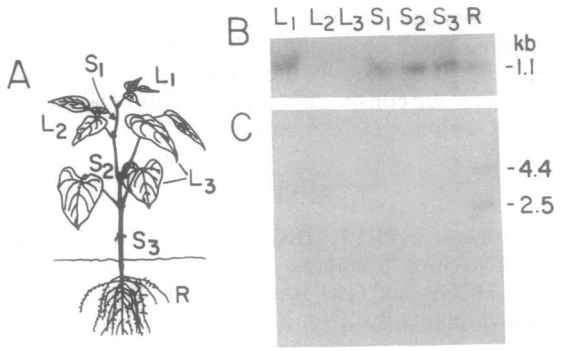

FIG. 3. PvPRP1, GRP, and HRGP mRNA levels in 3-week-old plants. L1, L2, and L3, young, expanding, and fully mature leaves, respectively. Stem sections S1, S2, and S3 were sectioned as illustrated. R, root. Blot was hybridized with the PvPRP1 probe (*B*) and rehybridized with the HRGP probe (*C*).

the 8-hr samples, where the immediately adjacent elongating zone shows much lower levels of this mRNA. The PvPRP1 mRNA was also induced 4-fold in the M_1 and M_2 segments within the mature zone, 5-fold in epicotyls, and 2-fold in cotyledons (8-hr samples in Fig. 4*B*; data not shown). The GRP1.8 mRNA was maximally induced in the M_2 segment, while the GRP1.0 mRNA was maximally induced in the hook, similar to the PvPRP1 mRNA (Fig. 4*C*).

The most dramatic induction of all four HRGP mRNAs occurred in the M_2 segment, while they remained extremely low in the hook (Fig. 4*C*). At 8 hr, the predominant 4.4-kb mRNA was 70 times the dark levels in M_2 and only 2 times the dark levels in M_1. These data reveal that light induces PvPRP1, GRP, and HRGP transcripts with apparently similar kinetics but in different regions of the seedling.

Induction of PvPRP1, GRP, and HRGP mRNAs in Hypocotyls Is a Phytochrome-Mediated Process. To identify the photoreceptor(s) involved in light regulation, 6-day-old etiolated seedlings were exposed to different light treatments. RNA was analyzed from entire hypocotyls to allow for the spatial differences in light regulation of PvPRP1, GRP, and HRGP transcripts (Fig. 5 and Table 2). Illumination with white light for 24 hr resulted in the expected accumulation of PvPRP1, GRP, and HRGP mRNAs. When seedlings were irradiated with 2 min of red light and then returned to the dark for 24 hr, the PvPRP1 transcript level was 4 times higher than the dark control and the two GRP and four HRGP transcripts were induced as well. However, when the red light pulse was immediately followed by 6 min of far-red light, all of the mRNAs remained low. The longer exposure to far-red light was carried out to ensure maximal reconversion of phytochrome from the physiologically active far-red form to the inactive red form. Illumination for 4 min with far-red light alone before the dark period failed to induce any of the mRNAs hybridized. These data showing red light inducibility

Table 1. Relative abundance of PvPRP1, GRP, and HRGP mRNAs in different regions of light-grown 6-day-old bean seedlings

		Hypocotyl				
RNA	Root	M	E	A	Epicotyl	Cotyledon
PvPRP1	48 (2)	18 (20)	19 (20)	124 (150)	135 (20)	1 (3)
GRP1.0	16 (2)	0.8 (1.5)	1.5 (>10)	3 (>10)	3.5 (>20)	1 (1.5)
GRP1.8	82 (3)	42 (3)	13 (3)	30 (5)	4.5 (>5)	1 (ND)
2.5-kb HRGP	125 (5)	0.8 (3)	0.05 (ND)	0.05 (ND)	0.3 (>5)	1 (−3)
4.4-kb HRGP	910 (7)	85 (4)	7 (4)	9 (>20)	0.8 (>3)	1 (1.5)

Values measured by scanning densitometry of Northern blots were standardized to 1.0 for RNA levels in cotyledons. Values in parentheses indicate -fold difference compared to RNA levels in the same organ parts from dark-grown seedlings. ND, not determined; M, mature; E, 10-mm section just below A; A, apical 5-mm section below cotyledon.

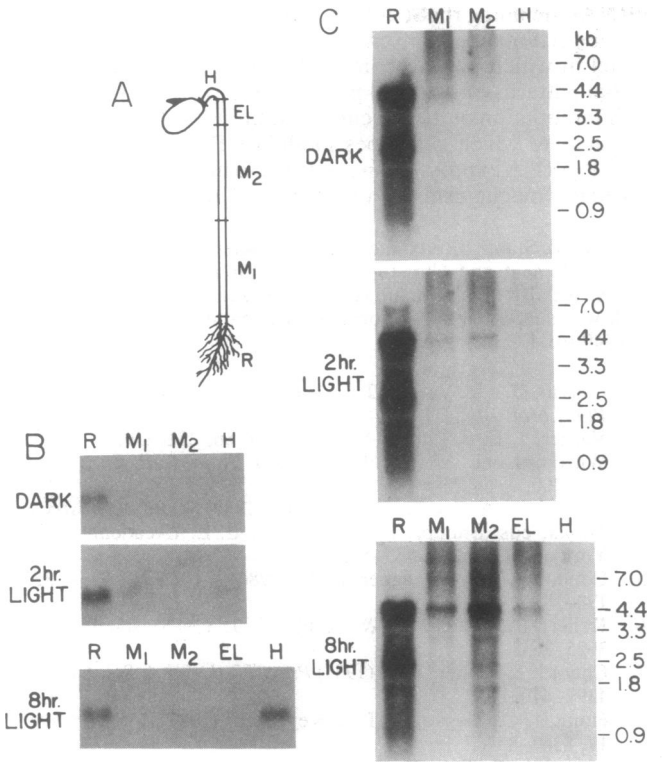

FIG. 4. Kinetics of induction of mRNAs by white light; 6-day-old etiolated seedlings were transferred to white light. (*A*) R, root; M_1 and M_2, lower half and upper half of the mature zone of hypocotyls; EL, 10-mm section below H; H, hook, which is the 10-mm section below the cotyledon. Blot was hybridized with the PvPRP1 probe (*B*) and rehybridized with the HRGP probe (*C*).

and far-red light reversibility demonstrate that phytochrome is involved in light regulation of all three classes of mRNAs. The kinetics of accumulation of all three classes of mRNA in etiolated seedlings illuminated with red light for 10 hr closely corresponded to the kinetics in white light (data not shown). However, illumination with a mixture of UV and blue light for 10 hr caused no significant induction of these mRNAs, suggesting that activation of UV and/or blue photoreceptors

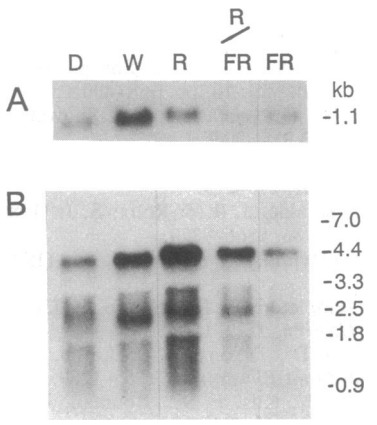

FIG. 5. Phytochrome-mediated induction of PvPRP1, GRP, and HRGP mRNAs; 6-day-old etiolated seedlings were exposed to different light conditions. Lanes: D, seedlings were kept in dark for 24 hr; W, seedlings were illuminated with white light for 24 hr. After exposure to the following light pulses, seedlings were returned to the dark for 24 hr: R, 2 min of red light; R/FR, 2 min of red light followed by 6 min of far-red light; FR, 4 min of far-red light. Blot was hybridized with the PvPRP1 probe (*A*) and rehybridized with the HRGP probe (*B*).

Table 2. Relative abundance of PvPRP1 and 4.4-kb HRGP mRNAs in hypocotyls of etiolated 6-day-old seedlings after different light treatments

	Dark	W	R	R/FR	FR
PvPRP1	1.0	11	4	0.6	0.5
4.4-kb HRGP	1.0	5	11.3	3.7	1.1

Values measured by scanning densitometry were standardized to 1.0 for RNA levels in the dark control. W, white light for 24 hr; R, 2 min of red light; R/FR, 2 min of red light followed by 6 min of far-red light; FR, 4 min of far-red light.

is insufficient for light regulation of these mRNAs (data not shown).

DISCUSSION

Etiolated seedlings display greatly elongated hypocotyls, the vascular systems are poorly developed, the leaves do not expand, and the plumular hooks open slowly, if at all. Illumination of etiolated seedlings results in many physiological changes, including alteration of cell expansion in different organs and vascular differentiation. This paper demonstrates that light induces the dramatic accumulation of mRNAs encoding a putative cell wall PRP and cell wall GRPs and HRGPs in different regions of seedlings. Moreover, the light-induced spatial patterns of mRNA expression differ from the patterns established in the absence of light.

Bean (6, 24) and soybean (13) GRP mRNAs have been localized to developing xylem cells in etiolated seedlings of approximately the same age as those we used. The cellular localization of PvPRP1 mRNA is unknown. In soybean, the three SbPRP gene family members exhibit differential regulation in the apical hypocotyls of etiolated seedlings (11, 14). SbPRP1 mRNA occurs in xylem and phloem. SbPRP2 mRNA is present mostly in phloem but also in pith and cortical cells. SbPRP3 mRNA is absent in the apical region but is present in the endodermoid layer in the elongating region. Analysis of 1-month-old plants showed that PRPs and GRPs are colocalized in lignified phloem and xylem in the stems of soybean and several Solanaceous species (12, 13).

We found that the PvPRP1 and both GRP mRNAs were more abundant in the mature region than the elongating and apical regions of 6-day-old etiolated seedling hypocotyls. In contrast, light-grown seedlings and etiolated seedlings exposed to several hours of light accumulated maximal levels of the PvPRP1 and GRP1.0 mRNAs in the apical region of hypocotyls and lower levels in the mature and elongating regions. Since our results demonstrate a similar regulation of PvPRP1 and GRP1.0 mRNAs in etiolated and light-grown seedlings, we hypothesize that the PvPRP1 mRNA may also be localized in developing primary vascular tissue. This hypothesis is further supported by the strong correlation between the prominent induction of PvPRP1 and GRP1.0 mRNAs in apical parts of the hypocotyl and the known transition from a low level of vascularization in the dark, which is least developed in the apical hypocotyl region, to a well-developed vascular system in the light. The validity of our hypothesis needs to be tested by PvPRP1 mRNA *in situ* hybridization or tissue printing studies.

Light is also known to stimulate radial growth of hypocotyls by increased cambial activity leading to the development of secondary vascular tissue. In etiolated 6-day-old soybean seedlings, HRGP mRNAs have been found primarily in the cambium as well as in a few layers of cortical cells surrounding the primary phloem (13). In light-grown 6-day-old seedlings, the HRGP mRNAs have been localized to the perivascular parenchyma cells of hypocotyls (25). We suggest that the light-induced increase of HRGP mRNAs primarily in the mature region of bean seedlings derived from expression in

the cambial layer as well as adjacent cortical cells. As postulated by Ye and Varner (13), the expression in cortical cells of HRGP mRNAs may be due to pressure or tensions on these cells caused by the expansion of adjacent vascular bundles.

We have shown that the levels of all three classes of mRNAs decreased in the epicotyls of seedlings maintained in the dark, whereas the mRNA levels remained at comparable levels in epicotyls of seedlings grown in the light. In the leaves of mature plants, the PvPRP1 and 4.4-kb HRGP mRNAs were detected in leaves, while the GRP mRNAs were not detected. Both SbPRP2 and HRGPs have been shown to be initially distributed in hypocotyl cortical cells of 2-day-old soybean seedlings and subsequently localized in vascular tissue (11–13, 21). Our findings suggest that the PvPRP1, GRP, and HRGP mRNAs may also be present in the relatively undifferentiated cells of the epicotyls of germinating seedlings. Continued growth in the dark may reduce expression in cortical cells, while light may induce expression in developing vascular cells.

Roots exhibited higher levels of all three classes of mRNAs in light-grown 6-day-old seedlings compared to etiolated seedlings. Soybean PRPs, GRPs, and HRGPs (12) and bean GRPs (6) have been previously localized in vascular tissue in roots. The higher level of these mRNAs in light-grown bean roots may reflect the more branched, better developed root system characteristic of light-grown plants.

Our work has also demonstrated differential regulation of individual transcripts of the GRP and HRGP gene families in response to light. The spatial expression of the GRP1.8 transcript was correlated with the major HRGP mRNA expression rather than with PvPRP1 and GRP1.0 mRNA expression. In contrast to the other two HRGP mRNAs, the 7.0- and 3.3-kb mRNAs were reduced in the hypocotyls of 6-day-old light-grown seedlings compared to etiolated seedlings. Similarly, HRGP mRNAs decreased in tomato seedlings after white light illumination and phytochrome mediated the responses (G. Dechamp-Guillaume, D. Rumeau, and M. T. Esquerre-Tugaye, personal communication). The modulation of specific GRP and HRGP transcripts suggests possible functional differences in the encoded proteins during cell wall assembly.

Several aspects of PRP, GRP, and HRGP mRNA regulation presented in this paper are similar to earlier studies of these mRNAs or their encoded proteins. Etiolated bean and pea seedlings exhibited gradients of cell wall hydroxyproline content (presumably reflecting HRGPs and/or PRPs) increasing with maturity of hypocotyls and epicotyls, respectively (26, 27). In addition, light-grown pea seedling shoots contained twice the level of cell wall hydroxyproline as their etiolated counterparts (27). Etiolated soybean seedlings also accumulated higher levels of a PRP mRNA and HRGP mRNAs in the mature region of hypocotyls compared to less mature regions, whereas GRP mRNAs showed the opposite distribution (28). Fennoy and Jones (29) found a gradient for certain HRGP mRNAs in etiolated cucumber seedlings similar to our HRGP mRNA distribution in bean but not in etiolated pea seedlings. Light had no effect on the HRGP mRNA levels in the limited shoot segments examined for either species.

Many processes in photomorphogenesis, including cell expansion and differentiation, have been shown to be phytochrome regulated (19). Our studies have shown that light regulation of mRNAs encoding all three classes of cell wall structural proteins is mediated by phytochrome in bean seedlings. The kinetics of mRNA induction we observed were similar to those of several other phytochrome-regulated mRNAs including rbcS, chlorophyll a/b binding protein, and chalcone synthase transcripts (18). Our studies support a model in which phytochrome activation results in different spatial patterns of cell wall protein gene regulation that lead to differentiation of the vascular system. Future studies need to elucidate which cell types modulate PvPRP1, GRP, and HRGP mRNA expression in response to light and identify the molecular mechanisms involved in light regulation.

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