Planta (1981) 153:267–272

Planta
© Springer-Verlag 1981

Action spectra for changes in the "high irradiance reaction" in hypocotyls of *Sinapis alba* L.

M.G. Holmes and E. Schäfer
Biologisches Institut II, Universität Freiburg, Schänzlestr. 1, D-7800 Freiburg/Br., Federal Republic of Germany

Abstract. Detailed action spectra are presented for the inhibition of hypocotyl extension in dark-grown *Sinapis alba* L. seedlings by continuous (24 h) narrow waveband monochromatic light between 336 nm and 783 nm. The results show four distinct wavebands of major inhibitory action; these are centred in the ultra-violet ($\lambda_{max}=367$ nm), blue ($\lambda_{max}=446$ nm), red ($\lambda_{max}=653$ nm) and far-red ($\lambda_{max}=712$ nm) wavebands. Previous irradiation of the plants with red light (which also decreases Ptot) causes decreased inhibitory action by all wavelengths except those responsible for the red light inhibitory response. Pre-irradiation did not alter the wavelength of the action maxima. It is concluded that ultra-violet and blue light act mainly on a photoreceptor which is different from phytochrome.

Key words: Blue light (photoreceptor) – Etiolation (reversal) – High irradiance reaction – Hypocotyl – Phytochrome – *Sinapis*.

Introduction

Plant photomorphogenetic response types can be divided into induction responses and so-called high irradiance responses (HIR). Induction responses are effected by a brief (i.e. minutes) red (R) or blue (B) light irradiation which can be reversed by subsequent irradiation with far-red (FR) light. Induction responses require relatively low light energies and obey approximately the Bunsen-Roscoe reciprocity law. The HIR responses usually require prolonged (i.e. hours) irradiation and do not exhibit reciprocity.

Abbreviations: B = blue; D = dark; FR = far-red; HIR = high irradiance reaction; HW = half power bandwith; Pr = R absorbing form of phytochrome; Pfr = FR absorbing form of phytochrome; Ptot = total phytochrome = Pr + Pfr; R = red; UV = ultra violet

Many HIR action spectra have been measured, the majority having been made with dark-grown plants (Mancinelli and Rabino 1978). The action spectra for dark-grown plants usually have action maxima in the B and FR wavebands (Hartmann 1967a) with either a shoulder (e.g. Mohr 1957; Siegelman and Hendricks 1957) or a peak (e.g. Jose and Vince-Prue 1977; Beggs et al. 1980) in the R waveband. Although the response to R light remains, the responses to continuous B and FR light vary with both age (Black and Shuttleworth 1974; Evans et al. 1965) and previous light treatment (Black and Shuttleworth 1974; Evans et al. 1965; Siegelman and Hendricks 1958; Turner and Vince 1969). In a recent report, Beggs et al. (1980) demonstrated that whereas hypocotyl growth in dark-grown *Sinapis alba* seedlings was inhibited by the B, R and FR wavebands, seedlings which had been grown under continuous white light (xenon arc source) were only strongly inhibited by radiation in the 550 to 700 nm waveband. Two 5 min pre-irradiations of previously dark-grown plants with R light were adequate to reduce substantially the subsequent response of the seedlings to the B and FR wavebands. Although the reduced response to B and FR light correspond with the concomitant loss of total phytochrome (Ptot), several questions remained open. Of these questions, we attempt here to determine (a) the spectral characteristics of the ultra-violet (UV) photoreceptor, (b) whether the loss of the FR inhibition maximum of dark-grown plants is due to a shift in spectral sensitivity or is merely reduced following pre-irradiation with R light (see Discussion) (c) whether the loss of the B and FR peaks following irradiation with R light is related to the same photoreceptor and (d) the fine structure of the FR inhibition peak.

Several approaches are suitable for answering these problems, but none are better than the measurement of detailed spectral responsivity curves for a

0032-0935/81/0153/0267/$01.20

given photoresponse. In this instance, the inhibition of hypocotyl elongation in *Sinapis alba* L. seedlings by monochromatic light in the 336 nm to 783 nm waveband is used as an assay system. The use of very narrow bandpass (half-power bandwith ~ 8 nm) interference filters permits identification of the fine structure of the spectral sensitivity of the plant. It also enables detection of small changes in sensitivity which may easily be masked using broad bandpass filters.

Materials and methods

Sinapis alba L. seeds (Asgrow Co., Freiburg-Ebnet, FRG; harvest 1975) were selected and sown on filter paper in plastic boxes, as described by Mohr (1966) except that a modified Hoagland's solution (Cumming 1967) was used instead of distilled water. The seeds were then transferred to darkness at 25° C until the pre-treatments shown in the Table were given. At the end of the pre-treatment, i.e. 54 h after sowing, all seedlings excluding the dark-grown plants received 5 min FR light and were then transferred to the monochromatic wavelength stations for 24 h at 25° C. Because the pre-treatments affect the lengths of the plants at the start of the experimental period, individual control plants were used for each pre-treatment, both at the beginning and at the end of the experiment; all control plants for 78 h except pre-treatment D received 5 min FR light at 54 h after sowing before being placed in the dark at 25° C for 24 h. A 5 min pre-treatment with FR alone at 54 h after sowing had no effect on the subsequent growth rate of dark-grown seedlings either in darkness or in B, UV, R or FR light.

The effects of the various treatments are expressed as percentage inhibition which is calculated as the suppression of elongation growth under each monochromatic wavelength relative to growth in darkness, i.e.

$$\text{Percentage inhibition} = \frac{\Delta D - \Delta\lambda}{\Delta D} \cdot 100\%$$

where ΔD and $\Delta\lambda$ = hypocotyl growth (in mm) in darkness and in monochromatic light, respectively, during the 24 h treatment period.

Hypocotyls of dark-grown control plants were typically 24 mm long at the start and 49 mm long at the end of the treatment period. Twenty-five seedlings were used for each treatment; after measurement of hypocotyl length the longest two and shortest six (non-germinated counting as short) were rejected, leaving 17 seedlings per treatment. Every value in Figs. 1 and 2 represents a minimum of 12 replicate treatments.

Light sources. Monochromatic light was filtered from Leitz-Wetzlar projectors fitted with Osram XBO 450W Xenon arcs (for wavelengths below ca. 550 mn; see Mohr and Schoser 1960) or specially constructed projectors fitted with Osram 500W 110V bulbs (above ca. 550 nm; see Mohr and Schoser 1959).

For higher fluence-rates, it was also necessary to use Zeiss Ikon Xenosol III projectors fitted with Osram XBO 2.5 kW Xenon arc lamps and appropriate mirrors (for details, see Raschke 1967).

Schott (Schott & Gen., Mainz, FRG) interference filters and colour filters were used at all wavelengths. Half power bandwidth (HW) of the filter combinations varied between 7 nm and 13 nm. The wavelength of maximum transmission was measured for each wavelength because the manufacturer's data were found to be unreliable. The following filter combinations were used for the fluence-rate response curves and are typical combinations for the filters in these wavebands. 367 nm (HW = 8 nm) = Schott UV-IL + KG1 (2 mm) + UG1 (3 mm) + BG38 (2 × 4 mm). 446 nm (HW = 10 nm) = Schott DEPIL + Schott AL + KG1 (5 mm) + BG38 (2 × 4 mm); for higher fluence-rates (square symbols in Fig. 2b), the DEPIL filter was omitted resulting in a HW of 25 nm. 653 nm (HW = 9 nm) = Schott DIL + RG 610 (3 mm) + KG1 (2 mm); for higher fluence-rates (square symbols in Fig. 2c), a Schott DAL substituted the DIL, giving a HW = 15 nm. 712 nm (HW = 10 nm) = Schott DEPIL + RG 695 + KG1 (2 mm); for higher fluence-rates (square symbols in Fig. 2d), a Schott IL substituted the DEPIL, giving a HW = 12 nm.

The R light source used in the pre-treatments (λ_{max} = 656 nm; 3.7 µmol $m^{-2}s^{-1}$) is described in detail by Mohr et al. (1964). The FR light source (λ_{max} = 740 nm; 21.0 µmol $m^{-2}s^{-1}$ is described by Mohr (1966). The spectroradiometer system, radiometer and reference standard used for all light measurements are described by Beggs et al. (1980). A thermopile was also used for cross-reference and for making measurements in the UV waveband.

Results

The inhibitory effect of 2.0 µmol $m^{-1}s^{-1}$ monochromatic light on hypocotyl growth of dark-grown seedlings was measured at 35 individual wavelengths between 336 and 783 nm (Fig. 1). Photon fluence-rate response curves were then measured at the major ac-

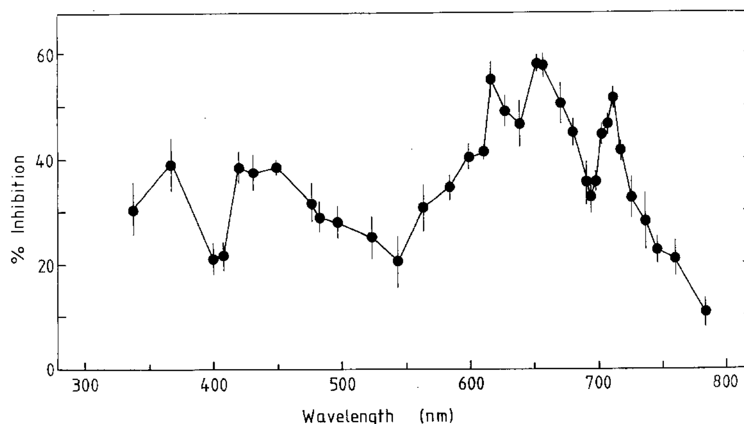

Fig. 1. Responsivity spectrum for the inhibition of hypocotyl elongation in dark-grown *Sinapis alba* L. seedlings by continuous (24 h) monochromatic light at a photon fluence-rate of 2.0 µmol $m^{-2}s^{-1}$. The vertical bars represent the standard error

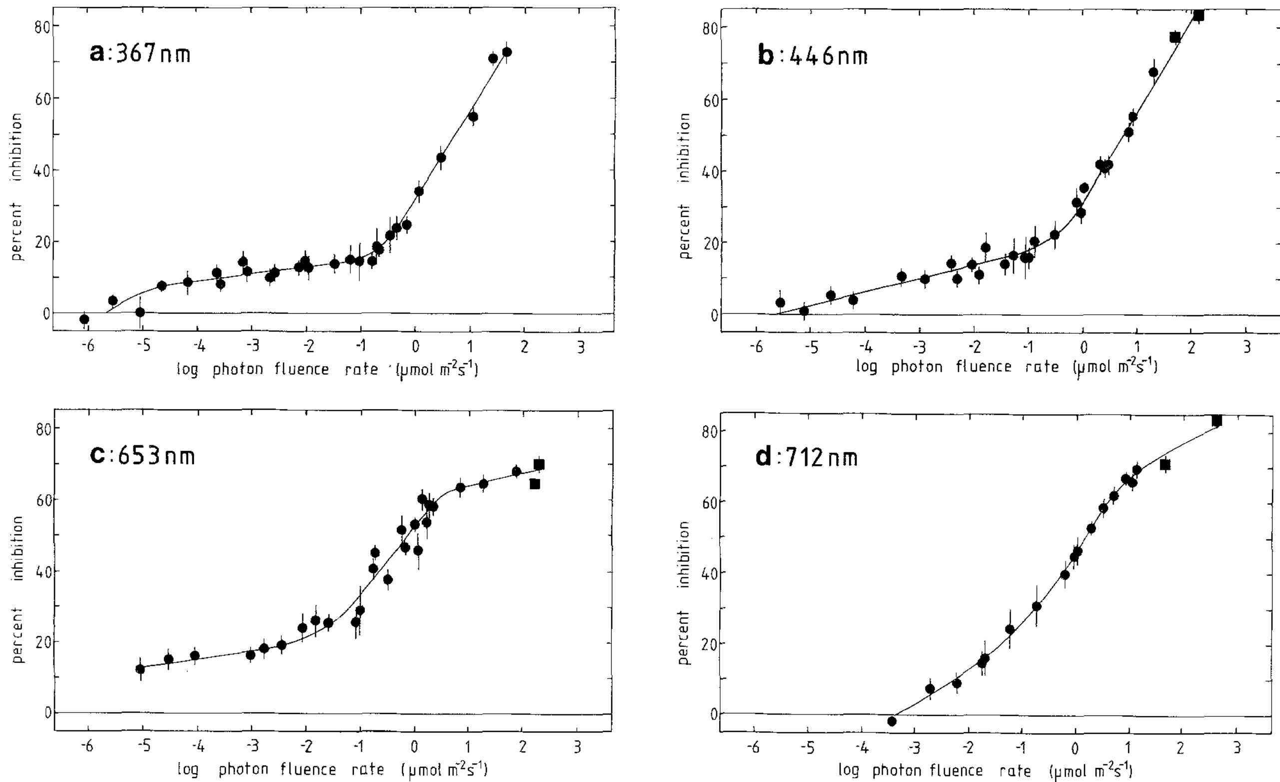

Fig. 2a–d. Photon fluence-rate response curves for the inhibition of hypocotyl elongation in dark-grown *Sinapis alba* L. seedlings by continuous (24 h) monochromatic light with the indicated wavelengths. The vertical bars represent the standard error. ● narrow bandpass filter combination; ■ broad bandpass filter combination; for details, see Materials and methods

tion maxima of 367, 446, 653 and 712 nm. Within the limits of resolution, the four photon fluence-rate response curves fall into three classes. The UV (Fig. 2a) and B (Fig. 2b) wavelengths appear to be identical. Inhibition starts at approximately 10^{-5} or 10^{-4} μmol $m^{-2}s^{-1}$ although there is negligible fluence-rate dependence (i.e. inhibition is constant at ca. 10%) until photon fluence-rates above 10^{-1} μmol $m^{-2}s^{-1}$ are used, when a log-linear relationship between photon fluence-rate and response is observed up to the highest inhibition measured (UV=73%; B=83%).

The response to R light (Fig. 2c) is similar to UV and B radiation in that it causes a marked but greater inhibition (ca. 15%) which does not vary over a wide range of low light levels. R differs from UV and B in that the fluence-rate dependency starts at lower light levels (ca. 10^{-2} μmol $m^{-2}s^{-1}$) and approaches saturation at a relatively low photon fluence-rate (ca. $10^{0}-10^{1}$ μmol $m^{-2}s^{-1}$). Also, it was not possible to achieve more than 70% inhibition with R light, even at 195 μmol $m^{-2}s^{-1}$; with UV or B, this inhibition was obtained at 30 μmol $m^{-2}s^{-1}$.

The FR curve (Fig. 2d) differs from all the others in that there is no fluence-rate independent phase at low light levels and that over 10^{-3} μmol $m^{-2}s^{-1}$ are required to obtain a measureable response. The fluence-rate dependence is maintained until at least 10 μmol $m^{-2}s^{-1}$; the indication of decreased effectiveness above this level may be due to the decreased effectiveness of the broader bandpass filters used at higher photon fluence-rates (see below).

To construct the action spectra, the appropriate photon fluence-rate response curves were superimposed over the response to 2.0 μmol $m^{-2}s^{-1}$ monochromatic light. The photon fluence-rate required for various degrees of inhibition was then interpolated from the curve. The photon fluence-rate response curves for 367 nm were used for the 336 to 400 nm waveband, the 446 nm curves for the 408 to 497 nm waveband, the 653 nm curves for the 524 nm to 679 nm waveband and the 712 nm curves for the 690 to 783 nm waveband. The suitability of this approach was tested by comparing the effects of using the response curve for two wavelength stations into the adjacent wavebands (e.g. using the 653 nm curve for the 694 nm wavelength); if this was done, no significant difference was observed in the shape of the action spectra. If, however, more distant wavelengths were calculated by this method (e.g. using the 653 nm curve for the 708 nm wavelength) the action spectrum was distorted. Because the shape of the photon fluence-

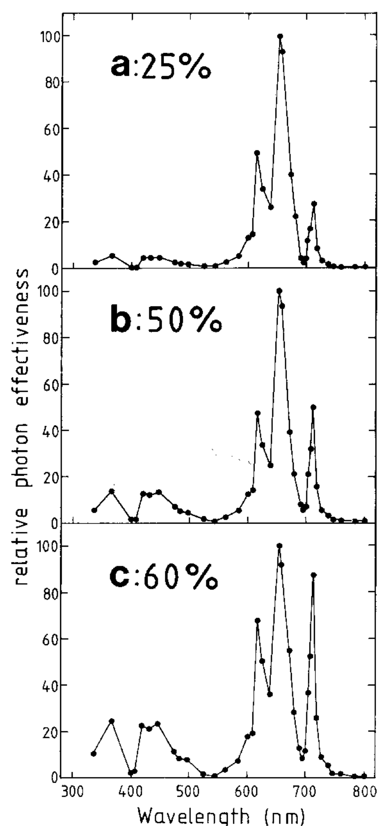

Fig. 3. Action spectra for the inhibition of hypocotyl elongation in dark-grown *Sinapis alba* L. seedlings by continuous (24 h) monochromatic light. The spectra were calculated by placing the responsivity data from Fig. 1 on the response curves of Fig. 2, using the reciprocal of the photon fluence rate required for 25%, 50% and 60% inhibition

rate response curves differs between wavebands, action spectra were calculated for 25%, 50% and 60% inhibition (Fig. 3). The general responses to all wavelengths are similar to those observed by Beggs et al. (1980). Additional features are evident, however, due to the use of very narrow bandpass filters and the

Table 1. Pretreatments used for the results presented in Fig. 4. λ = irradiation for 24 h (54–78 h after sowing) with continuous monochromatic light

Code	Pretreatment
D	54 h D; λ
Z	53.5 h D; 5 min R; 25 min D; 5 min FR; λ
Y	53 h D; 5 min R; 25 min D; 5 min R; 25 min D; 5 min FR; λ
X	52 h D; 5 min R; 55 min D; 5 min R; 55 min D; 5 min FR; λ

extension of the study into the UV waveband. It can be seen that the relative photon effectiveness is negligibly affected where the waveband of absorption is broad (e.g. 653 nm) and the wavelength dependence of the Pfr/Ptot ratio is small, but greatly accentuated where the wavelength dependence of Pfr/Ptot is high (c.f. 694 nm and 712 nm).

The major points which were not evident in the action spectrum of Beggs et al. are that there is also a peak of action at 367 nm and that the previously observed shoulder in the yellow-orange waveband is clearly a narrow bandwidth peak with an action maximum near 616 nm; the points at either side are at 609 and 625 nm. It is noteworthy that the relative spectral sensitivity of the various wavebands depends strongly on the degree of response being considered, even though saturation of the inhibitory effect was not reached.

The effects of the pre-treatments with R light (Table 1) on spectral sensitivity are presented for 50% inhibition in Fig. 4. Whereas the photon fluence-rate response curves for dark-grown plants were measured in detail over a wide range of fluence rates (Fig. 2), the curves for the pre-treatments X, Y and Z were restricted to the range required for construction of the action spectra. The data in Fig. 4 are normalised to 100% at the wavelength of maximum effectiveness to aid comparison between wavebands. These pre-

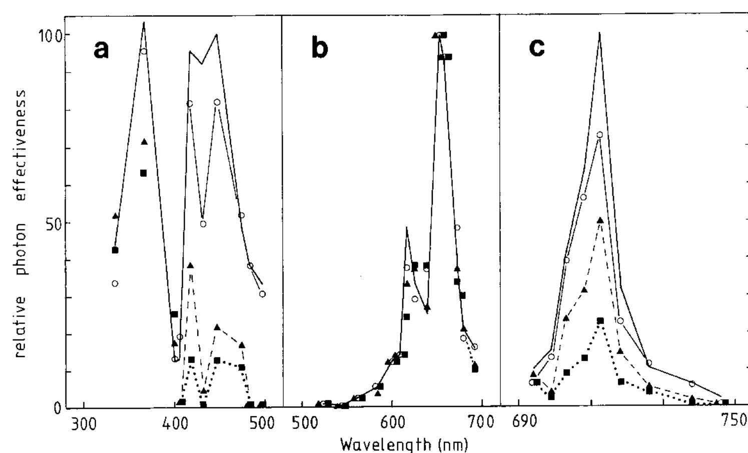

Fig. 4a–c. Action spectra for 50% inhibition of hypocotyl elongation in *Sinapis alba* L. seedlings. The data are normalised to a relative photon effectiveness of 100 at 446 nm (**a**), 653 nm (**b**), and 712 nm (**c**) to aid comparison. Continuous line = dark-grown seedlings; ○ pre-treatment Z; ▲ pre-treatment Y; ■ pre-treatment X

treatments have no significant effect on the subsequent response of the seedlings to light in the 500–700 nm waveband. This contrasts with the marked reduction in the effectiveness of the B and FR wavebands and, to a lesser extent, the UV waveband.

Discussion

The FR waveband . There is good evidence (Hartmann 1966; 1967a, b) that phytochrome alone is the pigment responsible for the FR action peak in dark-grown seedlings. The loss of the FR peak following pre-irradiation with R light (Fig. 4c) appears to support this concept. Based on Hartmann's model (Hartmann 1966) and Eq. (6) in the same publication, a R light pre-treatment reduces Ptot and therefore causes an increase in the parameter Kp ($Kp = k_2/k_1 \cdot [P]_o$ where, in this instance, k_1 and k_2 are the specific rate constants for the formation and decay of the PfrX complex respectively, and $[P]_o$ is the concentration of phytochrome before irradiation). Using a ratio of irradiation time: half-life of destruction of 20, we calculate an optimal predicted response at a photoequilibrium of ca. 0.12 for dark-grown seedlings assuming $Kp = 0.035$ (see Hartmann 1966). Reducing Ptot by a factor of 10 results in a predicted action maximum at $\varphi = 0.23$; reducing Ptot by a factor of 100 should produce an action maximum at $\varphi = 0.36$. In other words, progressive decreases in Ptot should cause a concomitant shift in the FR peak to lower wavelengths. The use of very narrow band-pass filters shows that this is not the case here and that the FR action maximum remains constant, at least when the Ptot content is reduced to ca. 20% (pre-treatment X; Beggs et al. 1980) of the dark level at the start of the treatment period.

Although such data are inconclusive without detailed time-course measurements of phytochrome throughout the entire treatment period for all pre-treatments, they do suggest that the mechanism proposed by Hartmann is inadequate even if the involvement of phytochrome is correct. A possibility which cannot be excluded is that the light pre-treatments alter the sensitivity of the system to subsequent light. If the FR peak does represent phytochrome action, then an explanation also has to be found for the fact that only 70% inhibition of growth can be produced by R light operating through phytochrome (Fig. 2c) whereas over 80% can be obtained by FR light (Fig. 2d) and saturation of the response has still not been reached.

The R waveband. Phytochrome appears to be the photoreceptor responsible for the R light action (Mancinelli and Rabino 1978). The possible involvement of chlorophyll has been rejected (Beggs et al. 1980). Two important points, namely the high sensitivity to 653 nm light and the separate peak at 616 nm, deserve attention.

Photon fluence-rates as low as $1.0 \cdot 10^{-5}$ µmol $m^{-2}s^{-1}$ produce substantial (12%) inhibition of growth even though photoconversion of Pr to Pfr is not spectrophotometrically detectable in *Sinapis alba* at 25° C below $1.0 \cdot 10^{-2}$ µmol $m^{-2}s^{-1}$ (Heim and Schäfer, unpublished data). This demonstrates that the seedling is either sensitive to very low levels of Pfr or that the Pfr is compartmentalised in relatively high concentrations.

The two distinct action maxima are observed at 616 nm and 653 nm; the minimum is near 639 nm. The double peak structure may be due to three causes. The first is that it is the product of differential screening within the tissues and differential absorption by phytochrome in the R waveband. The second possible cause is the presence of two R light photoreceptors. The third possibility is that the double peak of sensitivity represents two different electronic excitation bands of Pr; these are the Q_y band at 660 nm and the Q_x band near 610 nm (Song et al. 1979 and pers. comm.). Strongly marked maxima and minima have been observed previously in this waveband in both monocots and dicots (Vanderhoef et al. 1979).

The B waveband . The B portion of the responsivity spectrum resembles the action spectrum for inhibition of hypocotyl growth in *Lactuca* (Hartmann 1967a) although it lacks the fine triple-peaked structure observed by Hartmann. The B action maximum for control of hypocotyl growth has variously been described as being due to phytochrome and being due to a distinct B-sensitive photoreceptor. Detailed argument for phytochrome as the B photoreceptor has primarily been based on growth studies of *Lactuca* (Hartmann 1966, 1967a, b) and some evidence exists to support this suggestion in *Sinapis* (Wildermann et al. 1978). Conversely, there is evidence obtained with *Cucumis* (Meijer 1968) and *Lactuca* (Turner and Vince 1969) which indicates that the B light response is due to at least the partial interference of a separate photoreceptor.

The fluence-rate dependent portion of the 446 and 712 nm response curves are approximately parallel and differ only in that the response to B light requires a 3 to 4 fold greater photon fluence-rate than that to FR light. These wavebands are also similar in that, unlike the R waveband, their effectiveness is reduced by pre-irradiation with R light both at a similar rate and to a similar extent. They also differ from the R waveband in that the photon fluence-rates used

did not result in a saturation of the response. However, if the data for the B and FR wavebands are compared on the basis of the phytochrome photoconversion properties of the actinic light (Fukshansky et al., unpublished data) the response to B light cannot be accounted for in terms of phytochrome alone.

Although the response to B light appears to be due predominantly to a specific B light photoreceptor, a small part of the response may result from phytochrome action. There are three reasons for this. First, B light is effective in photoconverting Pr to Pfr in vivo at 25° C (Jabben et al., unpublished data); the fluence-rate independent portion of the curve may represent the response to low levels of Pfr. Second, the filter combinations used for producing photon fluence-rates of 55 and 145 μmol $m^{-2}s^{-1}$ transmitted up to 0.03% of the total energy above 600 nm; this visibly R component was probably sufficient to cause some inhibition via the highly sensitive R light absorbing pigment. Third, at photon fluence-rates above approximately 2.0 μmol $m^{-2}s^{-1}$, the seedlings irradiated with B light were visibly R when observed with the dark-adapted eye through a colour glass which transmits only above 600 nm. This appears to be due to fluorescence of protochlorophyll or chlorophyll formed during the treatment period because no R light could be detected in the light source itself by the same means. As the brightness of the seedlings was subjectively the same as those being irradiated with 653 nm light at $1.0 \cdot 10^{-2}$ μmol $m^{-2}s^{-1}$, some inhibition by fluoresced light is to be expected even if two orders of magnitude overestimation by this method is assumed.

The UV waveband. The photon fluence-rate response curves for 367 nm and 446 nm radiation are identical within the limitations of measurement error. Also, both wavebands show a loss in effectiveness following pre-irradiation with R light, although this is less marked at 367 nm. Although the amount of data for the UV waveband is limited, those presented suggest that the same pigment is responsible for the UV and B response and that only a small part of the response can be ascribed to phytochrome.

Supported by a grant to E.S. by the Deutsche Forschungsgemeinschaft (SFB 46). M.G. Holmes was supported by the Deutsche Forschungsgemeinschaft (Biologie der Zeitmessung Wa. 263/9). The authors are indebted to Inge Schomerus for her excellent technical help, to Dr. Leonid Fukshansky for discussion and criticism and to Max Seyfried for speedy service with the computer.

References

Beggs, C.J., Holmes, M.G., Jabben, M., Schäfer, E. (1980) Action spectra for the inhibition of hypocotyl growth by continuous irradiation in light and dark-grown *Sinapis alba* L. seedlings. Plant Physiol. **66**, 615–618

Black, M., Shuttleworth, J.E. (1974) The role of the cotyledons in the photocontrol of hypocotyl extension in *Cucumis sativus* L. Planta **117**, 57–66

Cumming, B.G. (1967) Early-flowering plants. In: Methods in developmental biology, pp. 277–299, Wilt, F.H., Wessels, N.K. eds., Thomas Y. Crowell Company, New York

Evans, L.T., Hendricks, S.B., Borthwick, H.A. (1965) The role of light in suppressing hypocotyl elongation in *Lettuce* and *Petunia*. Planta **64**, 201–218

Hartmann, K.M. (1966) A general hypothesis to interpret "high energy phenomena" of photomorphogenesis on the basis of phytochrome. Photochem. Photobiol. **5**, 349–366

Hartmann, K.M. (1967a) Ein Wirkungsspektrum der Photomorphogenese unter Hochenergiebedingungen und seine Interpretation auf der Basis des Phytochroms (Hypokotylwachstumshemmung bei *Lactuca sativa* L.). Z. Naturforsch. **22b**, 1172–1175

Hartmann, K.M. (1967) Photoreceptor problems in photomorphogenic responses under high energy conditions (UV-blue-far red). Abstracts European Photobiology Symposium Hvar Yugoslavia 29–32

Jose, A.M., Vince-Prue, D. (1977) Action spectra for the inhibition of growth in radish hypocotyls. Planta **136**, 131–134

Mancinelli, A.L., Rabino, I. (1978) The "high irradiance responses" of plant photomorphogenesis. Bot. Rev. **44**, 129–180

Meijer, G. (1968) Rapid growth inhibition of gherkin hypocotyls in blue light. Acta Bot. Neerl. **17**, 9–14

Mohr, H. (1957) Der Einfluß monochromatischer Strahlung auf das Längenwachstum des Hypokotyls und auf die Anthocyanbildung bei Keimlingen von *Sinapis alba* L. (= *Brassica alba* Boiss.). Planta **49**, 389–405

Mohr, H. (1966) Untersuchungen zur phytochrominduzierten Photomorphogenese des Senfkeimlings (*Sinapis alba* L.). Z. Pflanzenphysiol. **54**, 63–83

Mohr, H., Schoser, G. (1959) Ein Interferenzfilter Monochromatoranlage für photobiologische Zwecke. Planta **53**, 1–17

Mohr, H., Schoser, G. (1960) Eine mit Xenonbögen ausgerüstete Interferenzfilter Monochromatoranlage für kurzwellige sichtbare und langwellige ultraviolette Strahlung. Planta **55**, 143–152

Mohr, H., Meyer, U., Hartmann, K. (1964) Die Beeinflussung der Farnsporen-Keimung *Osmunda cinnamomea* (L) und *O. claytoniana* (L) über das Phytochromsystem und die Photosynthese. Planta **60**, 483–496

Raschke, K. (1967) Eine Anlage zur monochromatischen Bestrahlung biologischer Objekte ausgerüstet mit Interferenzfiltern und einer elektronisch geregelten 2.5 KW Xenonlampe. Planta **75**, 55–72

Siegelman, H.W., Hendricks, S.B. (1957) Photocontrol of anthocyanin formation in turnip and red cabbage seedlings. Plant Physiol. **32**, 393–398

Siegelman, H.W., Hendricks, S.B. (1958) Photocontrol of anthocyanin synthesis in apple skin. Plant Physiol. **33**, 185–190

Song, P-S., Chae, Q., Garner, J.D. (1979) Spectroscopic properties and chromophore conformations of the photomorphogenic receptor: phytochrome. Biochim. Biophys. Acta **576**, 479–495

Turner, M.R., Vince, D. (1969) Photosensory mechanisms in the lettuce seedling hypocotyl. Planta **84**, 368–382

Vanderhoef, L.N., Quail, P.H., Briggs, W.R. (1979) Red light inhibited mesocotyl elongation in maize seedlings. II. Kinetic and spectral studies. Plant Physiol. **63**, 1062–1067

Wildermann, A., Drumm, H., Schäfer, E., Mohr, H. (1978) Control by light of hypocotyl growth in de-etiolated mustard seedlings. I Phytochrome as the only photoreceptor pigment. Planta **141**, 211–216

Received 8 May; accepted 6 June 1981