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High Irradiance Response Promotion of a Subsequent Light Induction Response in *Sinapis alba* L.

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Abstract. Relative quantum responsivity curves for inhibition of hypocotyl elongation in *Sinapis alba* L. seedlings previously grown in white light confirm that a marked "end of day" inhibition response can be induced by a monochromatic light treatment (30 min) at the end of the light period. In dark grown seedlings, however, no growth inhibition can be induced by a 30 min monochromatic light treatment. A prerequisite for an induction response appears to be a pretreatment with continuous light. Far red light is most effective with blue and red light showing a lesser effectiveness. The light pretreatment also shows a marked fluence rate dependency with respect to its ability to allow an induction response to manifest itself. The pretreatment required shows all the characteristics of a classical "HIR" response. The appearance of the effect in plants treated with the herbicide SAN 9789 seems to exclude chlorophyll as being the photoreceptor.

Key words: High irradiance response – Hypocotyl elongation – Photomorphogenesis – Phytochrome – *Sinapis*.

Introduction

It is possible to influence elongation responses in green plants by changes in the quality of a short light pulse given at the end of the daily light period. Downs et al. (1957) for example, showed that for both *Phaseolus vulgaris* L. and two species of *Ipomoea* internode elongation was stimulated if the daily light period was followed by a short period of far red light. This effect of far red light could be reversed by a subsequent pulse of red light and they therefore concluded that the response was ascribable to the pigment now known as phytochrome. Kasperbauer (1971) was able to repeat these observations for *Nicotiana tabaccum* L. and also drew attention to the possibility that this effect might be of importance in the response of plants to shading.

Recently Wildermann et al. (1978) extended these observations to young seedlings of *Sinapis alba* L. where they found that in light-grown seedlings an "end of day" far red light pulse led to an increase in hypocotyl growth when compared to control plants grown in white light and transferred to darkness after a red light pulse. Mohr (1957), however, had investigated the effect of short light pulses on *S. alba* seedlings which had been grown entirely in darkness. He was unable to detect any differences in hypocotyl growth between those plants which had received a short pulse of either red or far red light. Bertsch and Mohr (1965) were able to show that for light-induced anthocyanin synthesis in *S. alba* a red pulse was only slightly effective in inducing anthocyanin synthesis but if the seedlings had first received 12 h far red light the effectiveness of a subsequent red pulse was greatly increased. It appears, therefore, that a plant often required a light pretreatment before an inductive pulse becomes fully effective. This paper seeks to investigate this problem further and to characterise both the effect and the nature of the required pretreatment.

Materials and Methods

Sinapis alba L. seeds (harvest 1975) were obtained from Asgrow Co., Freiburg-Ebnet, FRG, and selected and sown on chromatogra-

Abbreviations: SAN 9789 = 4-chloro-5-(methylamino)-2-(α, α, α-trifluoro-*m*-tolyl)-3(2H)-pyridazinone; RG9 light = long wavelength far red light (Schott RG9 colour glass); FR = far red light; WL = white light; BL = blue light; RL = red light; D = darkness; P_{tot} = total phytochrome; P_{fr} = far red absorbing form of phytochrome; HSR = high irradiance response

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phy paper in plastic boxes as described by Mohr (1966) except that a modified Hoaglands solution (Cumming 1967) was used instead of distilled water. In order to obtain plants grown in white light but with very low chlorophyll levels the herbicide SAN 9789 (Norflurazon) was added to the Hoaglands solution at a final concentration of $5 \cdot 10^{-6}$ M (pretreatment H). This herbicide inhibits carotenoid synthesis thereby leaving chlorophyll open to photodestruction if the plants are grown in white light of sufficient fluence rate (Bartels and Hyde 1970; Frosch et al. 1979). Thus an essentially chlorophyll-free but white light grown plant is produced (Jabben and Deitzer 1978). Phytochrome modulated photomorphogenic responses so far tested have been shown to be not significantly influenced by this herbicide (Jabben and Deitzer 1979, Frosch et al. 1979).

Inhibition of hypocotyl elongation was measured for plants which received one of the four following pretreatments after sowing and before the inductive light pulse.

1. Pretreatment D
54 h D + 10 min RG9 light → induction.

2. Pretreatment X
52 h D + 5 min RL + 55 min D
+ 5 min RL + 55 min D + 10 min RG9 light → induction.

3. Pretreatment W
54 h WL + 10 min RG9 light → induction.

4. Pretreatment H
54 h WL + 10 min RG9 light → induction
in the presence of $5 \cdot 10^{-6}$ M SAN 9789.

All pretreatments and the subsequent 24 h dark period were given at 25° C. White light was obtained from Xenon arc lamps (Osram XBO 10 KW), the light from which was filtered through heat absorbing glass (3 mm KG 1 glass, Schott and Gen. Mainz, FRG) and 6 mm thick Thermopane glass. The photon fluence rate in the 400–800 nm waveband was 270 μmol $m^{-2}s^{-1}$.

The pretreatments produced either plants with high P_{tot} and low chlorophyll (D), low P_{tot} and low chlorophyll (X), low P_{tot} and high chlorophyll (W) or low P_{tot} and low chlorophyll (H). P_{tot} values for pretreatment X were 25% of the dark (D) level, those for pretreatment H being 2.5% of the dark level. It is assumed that the value for the green plants (W) was of the same order of magnitude.

After 54 h pretreatment all plants were given a saturating irradiation with RG9 light in order to establish a unified low P_{fr}/P_{tot} ratio (< 1%) and then irradiated with monochromatic light of wavelengths between 400 and 760 nm for 30 min. The photon fluence rate of this irradiation was in all cases 3.3 μmol $m^{-2}s^{-1}$. After this irradiation the plants were transferred to darkness at 25° C for a further 24 h.

After 24 h, the lengths of the hypocotyls were measured and percentage inhibition calculated as:

$$\frac{\text{Control II-Exp.}}{(\text{Control II} - \text{Control I})} \times 100$$

where Control I = length in mm of plants after 54 h under conditions of pretreatments D, X, W or H respectively.

Control II = length in mm of plants 54 h under pretreatment conditions followed by 10 min RG9 light and a further 24 h in darkness.

Exp. = length in mm of plants 54 h under pretreatment conditions followed by 10 min RG9 light + 30 min of the test wavelength and a further 24 h in darkness.

Typical control lengths were as follows:

	D	X	W	H
Control I	28.2 ±0.7	27.9 ±0.8	5.0 ±0.1	5.1 ±0.1
Control II	56.9 ±1.1	57.7 ±2.4	16.3 ±0.1	12.0 ±0.3

(where the errors indicate standard errors)

For experiments to investigate the nature of the pretreatment required for an induction response, plants were grown for 54 h under white, red, far red or blue light or for 48 h in darkness followed by 6 h in these light qualities (all standard sources). The inductive effect of 30 min red and that of 15 min RG9 light was measured after a further 24 h in darkness. A similar experiment involved the programme 48 h darkness + 6 hourly spaced 5 min red or far red light pulses as pretreatment.

In contrast to experiments shown in Fig. 1 a–d in these experiments (Fig. 3 and 4 and Tab. 1) % inhibition was not measured, because one would have to measure the control I and II for all various pretreatments. This was not possible because of the limited space for monochromatic and dichromatic irradiation. Furthermore the 30 min red were not preceeded by 10 min RG9 light (no differences could be seen in control experiments) and a 15 min RG9 light irradiation was used instead of 10 min RG9 light.

For some experiments the fluence rate of the 6 h light pretreatment was varied. The dichromatic curve was produced in the same way but with two light qualities (RL and RG9 light) being superimposed in the pretreatment, the fluence rate of the red light being varied.

Light sources and their measurement were as described previously (Beggs et al. 1980) with the addition of standard blue (Hanke et al. 1969). Other light sources used are detailed in the relevant figure legends.

For the phytochrome measurements plants were grown in darkness for 54 h – according to pretreatment D, but without the terminating RG9 light – and then irradiated for 30 min, at a fluence rate of 3.3 μmol $m^{-2}s^{-1}$, with monochromatic light. The plants were kept at 25° C during the irradiation. Variations in the light treatment used for phytochrome measurements are given in the relevant figure legend. 24 cotyledons were then placed in ice cold cuvettes under a dim green safe light (Mohr and Appuhn 1963) and phytochrome measured using a modified ratiospect (Pratt and Marmé 1976).

Results

Figures 1 a and 1 b show the results obtained from pretreatments D and X which are essentially dark grown plants. No significant inhibition of hypocotyl elongation was found under any of the wavelengths tested. In the case of plants which received white light as pretreatment (pretreatments W and H), wavelengths between 550 and 690 nm have a strong inhibitory effect on hypocotyl elongation (Fig. 1 c and d). Wavelengths below 550 nm show a lesser but still significant inhibitory effect. In SAN 9789 treated plants, blue light appears to be more effective than

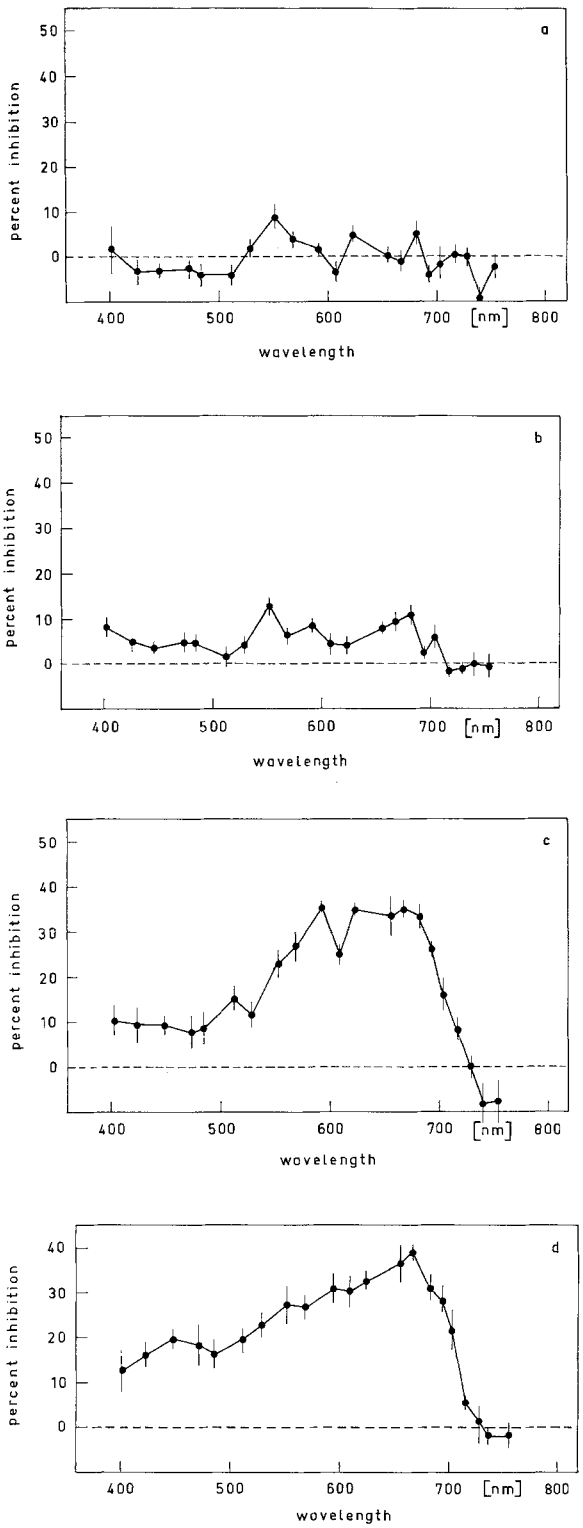

Fig. 1a–d. Plot of per cent inhibition of hypocotyl elongation against wavelength (relative photon responsivity). The inhibition was induced by 30 min light pulses 3.3 μmol $m^{-2}s^{-1}$ and measured after a 24 h dark period at 25° C. **a** Pretreatment D 54 h D+10 min RG9 light, **b** pretreatment X 52 h D+2× (5 min RL+55 min D)+10 min RG9 light, **c** pretreatment W 54 h WL+10 min RG9 light, **d** pretreatment H 54 h WL+10 min RG9 light in the presence of SAN 9789

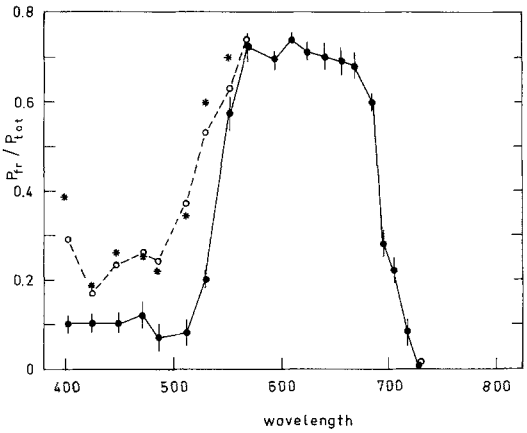

Fig. 2. P_{fr}/P_{tot} ratio established by 30 min irradiation plotted against wavelength. ●—●: irradiation at 3.3 μmol $m^{-2}s^{-1}$, *= irradiation at 33 μmol $m^{-2}s^{-1}$, ○—○=plants received 5 min red light to establish $P_{fr}/P_{tot}=0.75$ before 30 min irradiation at 3.3 μmol $m^{-2}s^{-1}$

in green plants. This effect is probably due to the lack of strong screening effects of chlorophyll and carotenoids in SAN 9789 treated plants.

We also investigated whether the responsitivity of the plants to the various wavelengths could be related to the percentage of phytochrome in the physiologically active P_{fr} form established by these wavelengths.

Figure 2 shows the P_{fr}/P_{tot} ratios established in dark grown seedlings after 30 min irradiation at 25° C plotted against the relevant wavelengths. Since photoconversion may be a limiting factor for wavelengths below 550 nm values were also determined after the fluence rate had been increased tenfold and also where the photoequilibrium was approached from a high P_{fr} level, that is where a saturating red light pulse was given before the seedlings were transferred to monochromatic light. The results show that part of the curve representing wavelengths above 550 nm is very close to that calculated by Hartmann on the basis of P_r and P_{fr} in vitro absorption spectra (Hartmann 1966). Below 550 nm however there are considerable differences. The P_{fr}/P_{tot} ratios are very much lower ($\simeq$0.1 as opposed to the values between 0.4 and 0.5 calculated by Hartmann and until now generally used) and even after irradiation with a 10fold higher fluence rate or after first irradiating with red light the final value reached was only around 0.2–0.3. Aspects of this problem will be dealt with in a forthcoming paper.

Since it appeared that a light pretreatment was necessary for the full induction effect to manifest itself, experiments were performed to investigate the nature of the required pretreatment. The results are shown in Table 1. It seems that regardless of whether the plants receive a 54 h or a 6 h preirradiation, the

Table 1. Differences (ΔL) between the inductive effect of a 30 min red and that a 15 min RG9 pulse on hypocotyl growth inhibition in *Sinapis alba* L. seedlings after various pretreatments. The pretreatment time was always 54 h and was followed by the irradiation. Measurements were made after a further 24 h in darkness. Light sources were standard sources

Pretreatment	Energy fluence rate of pretreatment (W m^{-2})	ΔL (mm)
54 h WL	74[a]	6.0
54 h RL	0.67	2.2
54 h FR	3.5	6.1
54 h BL	3.12	4.3
54 h D		−0.8
48 h D+6 h RL	2	4.4
48 h D+6 h FR	2	6.5
48 h D+6 h BL	2	3.3
48 h D+6×(5 min RL+55 min D)	0.67	0.9
48 h D+6×(5 min FR+55 min D)	3.5	2.7

[a] 450–900 nm waveband

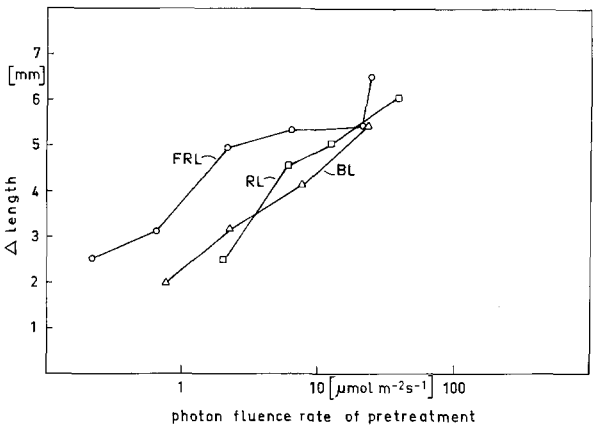

Fig. 3. Fluence rate response curves for the effect of a 6 h light pretreatment on the responsivity of the hypocotyl growth towards light pulses. The responsivity (ΔL) was analysed as difference in hypocotyl length after either a 15 min RG9 light or a 30 min RL pulse and a 24 h D period. ΔL is plotted against photon fluence rate of a 6 h light pretreatment. Light sources: Leitz Prado projectors with Osram 58 8880 E 500 W tungsten filament bulb (FR and BL) or fluorescent lamps Philips TL 40 W/15 (RL). Wavelengths were isolated with FR = Plexiglas PG 501 (3 mm) + PG 627 (3 mm), BL = Schott & Gen. DAL interference filter (λmax = 449 nm), RL = Plexiglas PG 501 (3 mm)

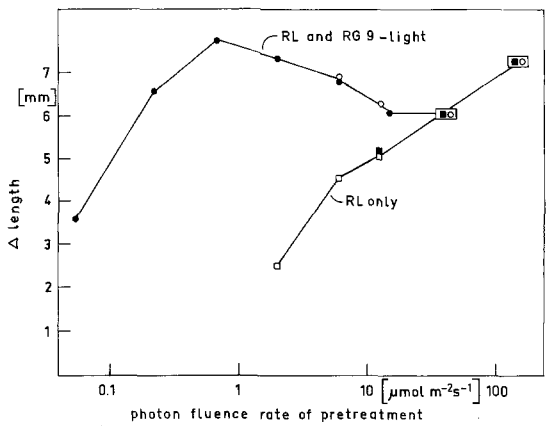

Fig. 4. Difference (ΔL) between induction effect of 30 min RL and 15 min RG9-light plotted against photon fluence rate of a 6 h light pretreatment. Red light was given alont (□, ■) or simultaneously with RG9-light (○, ●) at constant (12.7 μmol $m^{-2}s^{-1}$) photon fluence rate. Light sources for RL Philips TL 20 W/15 fluorescent tubes (white signs) or Zeiss Xenosol III + Schott AL 655 nm interference filter. For RG9-light always Prado projector (Fig. 3) with 5 min RG9 colour glass

most effective waveband is in the far red region with blue and red light somewhat less effective. Pulse treatment was ineffective when compared with the continuous light treatment.

Figure 3 shows the results of a test of the fluence rate dependence of the effect, i.e. fluence rate response curves for blue, red and far red light. In all cases the effect is clearly strongly fluence rate dependent. The stronger effectiveness of far red light is also confirmed. The resemblance of the effectiveness of the various wavebands to action spectra for high irradiance responses (Mohr 1957; Beggs et al. 1980) and the relatively low effectiveness of pulse treatment raised the question whether one is in fact dealing here with a high irradiance response. Figure 4 shows an experiment with dichromatic light where the fluence rate of the red light was varied between 0.02 and 50 μmol $m^{-2}s^{-1}$ against constant background of RG9 light at photon fluence rate of 12.7 μmol $m^{-2}s^{-1}$. It can be seen that with increasing fluence rate of red light a maximum of effectiveness is reached at a fluence rate where red light alone is relatively ineffective. The effectiveness of red light (dichromatic) then declines again with further increases in fluence rate (cf. Hartmann 1967b), confirming that one is dealing with a high irradiance response of the type described by Hartmann (1966, 1967a, b).

Discussion

The lack of any significant induced inhibition of hypocotyl elongation in dark-grown plants agrees with the results of Mohr (1957) showing that not only red and far red but also all other wavelengths are ineffective. However the results of Downs et al. (1957), Kasperbauer (1971) and Wildermann et al. (1978) are supported by the experiments with those plants receiving a white light pretreatment. In this case it can be seen that a wide range of wavelengths are effective in inducing inhibition.

The small minimum at 608 nm in green plants appears to be significant but cannot at present be

explained. It should be noted, however, that minima in this region have already been reported for light-induced elongation of etiolated pea (*Pisum sativum* L.) leaves (Parker et al. 1949) and light-induced promotion of elongation of protonemata of the fern *Onoclea sensibilis* L. (Miller and Miller 1967).

The photoreceptor for the inhibitory effect in both the blue and red wavebands appears to be phytochrome. When the inhibition of the hypocotyl growth is plotted against the P_{fr}/P_{tot} ratios established by various wavelengths (Fig. 5a and b) the amount of inhibition in both the green and SAN 9789 treated plants appears to be a function of the P_{fr}/P_{tot} ratio. The same relationship is observed in both the blue and red wavebands, implying that for the blue wavelengths no other photoreceptor is predominantly involved.

A continuous light treatment appears to be a prerequisite to produce an induction response. Pulsed light treatments were considerably less effective even though saturating from the point of view of establishing the P_{fr}/P_{tot} ratio. The results strongly imply that the pretreatment required is a classical high irradiance response (see Mancinelli and Rabino 1978).

The relative effectiveness of the various wavebands tested (far red, red, blue) show similarities to the action spectra for continuous irradiation responses for hypocotyl elongation inhibition in *Sinapis alba* L. (Mohr 1957, Beggs et al. 1980) and *Lactuca sativa* L. (Hartmann 1967a). The effect is furthermore strongly fluence rate dependent. These facts and those shown in Fig. 4 for dichromatic irradiation suggest that, at least as regards the red/far red region, phytochrome is probably the photoreceptor. Chlorophyll is unlikely to be involved as the effect was also apparent in SAN 9789 treated seedlings.

Various other effects of a light pretreatment on a later phytochrome response have been reported in the literature by Tanada (1972), Raven and Shropshire (1975). In these cases, however, the pretreatment consisted only of a red light pulse. In our experiments, red light pulses had only limited effectiveness on the appearance on an induction response. It seems more likely that the effect is of the same type as that reported by Bertsch and Mohr (1965) for the effect of a continuous far red light pretreatment on a subsequent red light pulse induced anthocyanin synthesis.

Indeed this effect appears to have been described several times in the literature but not necessarily recognized. Some if not all of the cases where a continuous blue light pretreatment leads to an increased red pulse induction effect (Mohr and van Nes 1963, Scherf and Zenk 1967, Kochhar et al. 1979, Mohr 1979) may well be in fact responses of the type described in this paper.

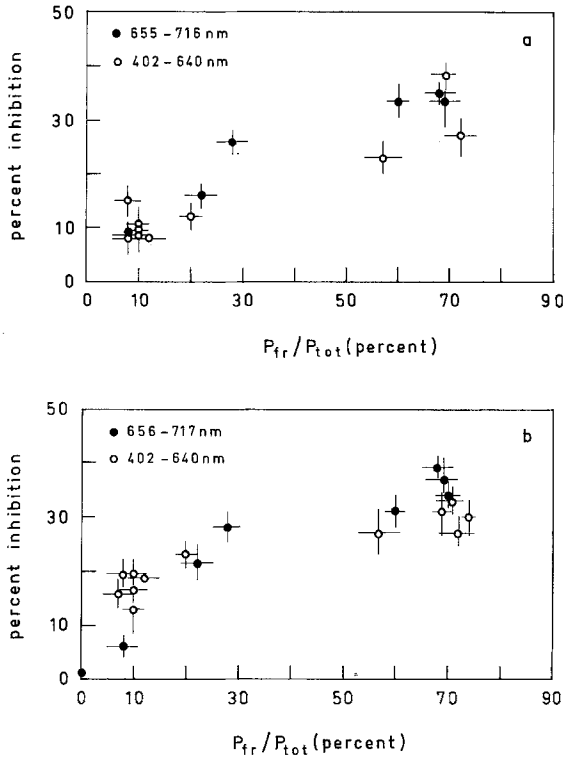

Fig. 5a, b. Per cent inhibition of hypocotyl elongation induced by a 30 min photon fluence rate of 3.3 $\mu mol\ m^{-2}s^{-1}$ plotted against P_{fr}/P_{tot} ratio established by the same light pulse in dark-grown seedlings. **a** Petreatment W (54 h WL), **b** pretreatment H (54 h WL in the presence of SAN 9789). Bars indicate standard errors

An important conclusion of this paper is that when a blue light pretreatment leads to an increased induction effect, this is not evidence for the involvement of a blue light receptor per se. It must first be checked whether far red and red light have the same effect and even if this is smaller than the effect of blue light it is still possible that one is dealing with a high irradiance response (Mancinelli and Rabino 1978, Mancinelli and Walsh 1979). Whether a specific blue light receptor is involved in the blue part of the HIR remains to date an open question.

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