Planta (Berl.) 67, 122—135 (1965)

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PHOTOCONTROL OF ANTHOCYANIN FORMATION IN TURNIP SEEDLINGS

II. THE POSSIBLE ROLE OF PHYTOCHROME IN THE RESPONSE TO PROLONGED IRRADIATION WITH FAR-RED OR BLUE LIGHT

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With 6 Figures in the Text

(Received July 6th, 1965)

Summary

The substitution of red or blue light for the first six hours of prolonged irradiation with far-red light reduced anthocyanin formation by about 60%; red or far-red light similarly substituted for blue light had little effect. It is concluded that the effects of prolonged irradiation with blue and far-red depend, in part at least, on different photoreceptors.

The effects of pre-treatment with red or blue light also occurred when only short exposures to light were given, and were reversed by immediate brief exposures to far-red. The depressing effect of a short pre-irradiation treatment was largely prevented if seedlings were kept at low temperature or in an atmosphere of nitrogen in the dark period before transfer to the prolonged far-red treatment. The effect of the pre-irradiation treatment is attributed to enzymatic destruction of phytochrome following conversion to the P_{FR} form, and it is suggested that anthocyanin synthesis in far-red light largely depends on phytochrome, possibly due to the maintenance of a low level of P_{FR} in the tissue by the absorption tail of P_R in the far-red.

A pre-irradiation treatment with red also decreased the inhibitory effect of far-red on hypocotyl elongation but did not change the response to blue light.

I. Introduction

The identity of the photoreceptor(s) involved in the responses of plants to prolonged high intensity irradiation with blue and far-red light is a matter of dispute. MOHR (1964) has suggested a single photoreceptor other than phytochrome. HENDRICKS (1960) and BUTLER et al. (1963) on the other hand, proposed that some of the effects of prolonged exposures to both blue and far-red are mediated through phytochrome. Another suggestion (HEATH and VINCE 1963) is that the far-red effects are brought about by the absorption of light by the phytochrome system whereas the blue effects are largely dependent on light absorbed by a second pigment. Because of the overlapping absorbancies of the two forms of phytochrome throughout most of the effective spectral regions (BUTLER et al. 1965) it has proved extremely difficult to determine how much of the effect of prolonged irradiation is due to phytochrome and how much to another reaction (the so-called "prolonged light reaction"

or "high-energy reaction"). MOHR (1964) attempted to separate the two reactions in the following ways. The effect of flashes of light separated by dark periods was assumed to be due entirely to phytochrome and was subtracted from the total effect obtained when light of the same wavelength was given continuously over the same period: the assumption that the prolonged light reaction is not affected by short flashes of light may not, however, be valid (SALE et al. 1964). Alternatively seedlings were given a background irradiation with red light during the prolonged irradiation; the response to the red background, when given alone, was ascribed to phytochrome and subtracted from the total response obtained when both were used together; however, as the ratio of P_{FR}:P_R at photo-equilibrium depends on the spectral distribution of the source (BUTLER et al. 1965) the phytochrome effect may vary according to the wave-length used for the prolonged irradiation.

The three regions of action for anthocyanin synthesis in turnip seedlings make them particularly suitable for studying possible interrelationships between the various light reactions; the action spectrum in prolonged high-intensity light has peaks in the far-red and blue (SIEGELMAN and HENDRICKS 1957) and there is also an effect of the reversible red/far-red reaction of phytochrome (GRILL 1965). Spectrophotometric measurements have shown that the apparent phytochrome content of etiolated seedlings falls sharply after exposure to red light (BUTLER and LANE 1965, DE LINT and SPRUIT 1963). We have already shown that a pre-treatment with red light depresses anthocyanin synthesis in prolonged far-red and suggested that phytochrome destruction might be involved (see VINCE 1964). In this paper the problem of the relationship between phytochrome and the "prolonged-light reaction" has been further investigated by studying the effects of red light and other pre-treatments on anthocyanin synthesis during prolonged irradiation with far-red or blue light.

II. Materials and methods

Seedlings of *Brassica rapa L.* "Red Globe" were grown on units of three microscope slides wrapped in filter paper (Whatman No. 1). These were either placed immediately in transparent plastic boxes ($14 \times 8 \times 6$ cm), or initially in trays ($43 \times 25 \times 8.5$ cm), which gave more uniform conditions for germination, and transferred to the plastic boxes after $1^1/_2$ days. Two units of 32—36 seedlings were placed in each box with 15 ml of de-ionised water or 5×10^{-3} M phenylalanine; while in trays the phenylalanine-grown seedlings received 2.5×10^{-3} M solution. Seedlings were grown in the dark for 24 to 60 hours before irradiating and anthocyanin content was measured as before (GRILL 1965) after 42 or 48 hours from the beginning of the main light treatment.

During the illumination treatments boxes were placed in the lighted cabinets described previously (GRILL 1965); unless otherwise stated the intensities were 6.0 Kergs cm^{-2} sec^{-1} in the blue, 3.6 in the red and 3.5 (between 700 and 800 nm)

in the far-red cabinet; the figure given for blue is a mean value as the intensity fell slightly during the long illumination periods, probably due to overheating of the fluorescent tubes.

The temperature was maintained at 25° C throughout or, in the high temperature treatment, was raised to 35° C overnight before the light treatments began, giving about nine hours at the high temperature. When low temperatures were required boxes were placed in a refrigerator at 2—6° C.

III. Experimental results

Irradiating dark-grown seedlings with red light would convert most of the phytochrome present to the P_{FR} form and result in a substantial loss of reversible phytochrome within a few hours: if the prolonged light reaction is mediated through a single photoreceptor independent of the phytochrome system such a pre-treatment with red light should not alter substantially the amount of anthocyanin formed after a subsequent irradiation with blue or far-red. The results of Fig. 1 show that, when a six-hour period in red light preceded a treatment of 42 hours in far-red, anthocyanin content was considerably less than in 48 hours far-red, even though six hours of red gave about the same yield of anthocyanin as six hours of far-red. A similar but somewhat smaller depression was obtained by a pre-treatment with six hours of blue light. In marked contrast is the almost total lack of effect when six hours of red preceded 42 hours in blue light. The effects of pre-irradiation were more or less independent of whether the seedlings were grown in phenylalanine or water, or pre-treated with high temperature, treatments that have been shown earlier to influence responsiveness to the red/far-red reversible reaction of phytochrome (GRILL 1965).

The large difference in the effect of the same pre-irradiation treatment with red on the amount of anthocyanin formed in response to prolonged irradiation with far-red or blue light suggests that the far-red and blue peaks of the "prolonged light reaction" for anthocyanin synthesis in turnip seedlings depend, in part at least, on different photoreceptors. As a treatment with red light is known to cause a marked loss of reversible phytochrome it is suggested that the action of far-red light in etiolated seedlings may depend on the phytochrome system and, in the following experiments, an attempt was made to determine whether the decreased anthocyanin synthesis after exposure to red or blue light is really brought about by phytochrome destruction in the tissue!

From previous work it appears that phytochrome content is increasing during the early stages of growth in darkness of turnip seedlings (GRILL 1965). If seedlings have not yet developed their full phytochrome content and are still capable of phytochrome synthesis they would be expected to be less affected by phytochrome destruction than older seedlings. In 24 hours old seedlings (Fig. 2) the depressing effect of a pre-irradiation

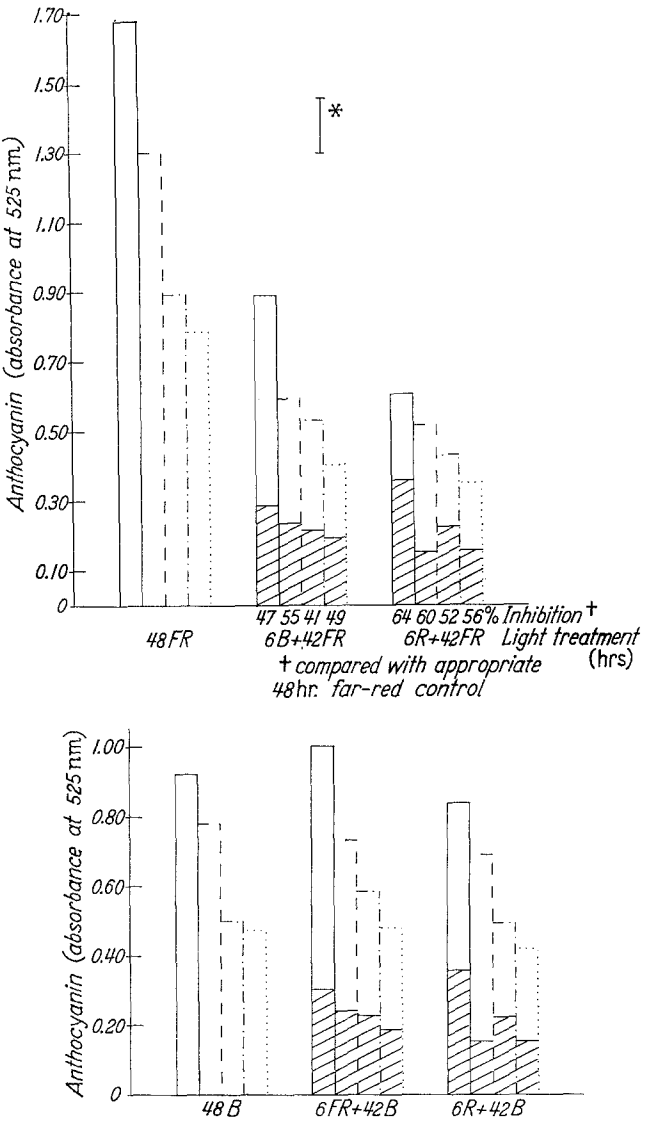

Fig. 1. The effect of a six-hour pre-irradiation treatment on anthocyanin formation in 42 hours of far-red or blue light. Seedlings were 48 hours old and grown in water (*W*) or phenylalanine (*P*) and were either kept at 25° C throughout or were transferred to high temperature 9 hours before starting the light treatments (*HT*). Controls received 48 hours of far-red or blue light. * Significant difference at $P = 0.05$. ——— HT.P.; — — — — P.; ·—·—·— HT. W.; ····· W.;
▨ Yield after the 6-hour pre-irradiation

period with either red or blue on anthocyanin synthesis in far-red was less than that found in the 48 hours old seedlings (Fig. 1), e.g. 35% depression by red in the younger seedlings compared with 56% in the older

seedlings, when both were grown in water without a high-temperature treatment. This reduced effect of pre-irradiation on young seedlings lends support to the suggestion that phytochrome destruction is involved, and may also imply that phytochrome synthesis is not markedly suppressed after an exposure to red light as was observed by BUTLER et al. (1965) in corn seedlings. The response to blue light was again not affected by a pre-irradiation with red.

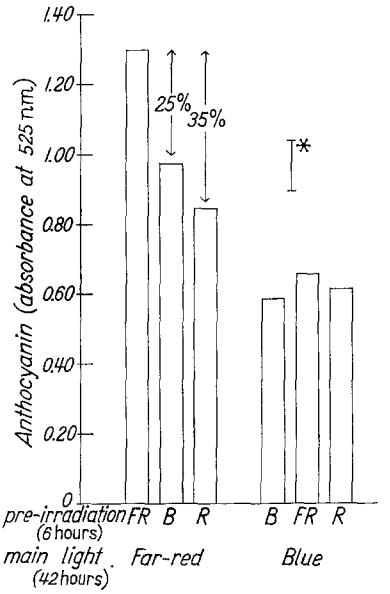

Fig. 2. The effect of a six hour pre-irradiation treatment on anthocyanin formation in 42 hours of far-red or blue light. Seedlings were 24 hours old and grown in water at 25° C throughout. Controls received 48 hours of far-red or blue light. * Significant difference at $P = 0.05$

As a single brief exposure to red light converts about 80% of the P_R present in etiolated tissue to P_{FR}, which then undergoes almost complete destruction in the following dark period (DE LINT and SPRUIT 1963, BUTLER et al. 1965) the continuous pre-irradiation periods were replaced by intermittent exposures to red or blue light; far-red reversibility was also investigated as phytochrome is thought only to undergo destruction when in the P_{FR} form. The pre-irradiation period with six hours of red or blue light was replaced by six exposures of 5 minutes, one at the beginning of each hour, the plants otherwise remaining in darkness. From Fig. 3 it is evident that intermittent exposures to red or blue were both effective in depressing anthocyanin synthesis in far-red: intermittent exposures followed by 42 hours of far-red resulted in 58% (red) and 44% (blue) inhibition of anthocyanin synthesis compared with 42 hours far-red. When each brief exposure to red or blue was followed by 5 minutes of far-red, the inhibiting effect was reduced but not entirely prevented; the far-red reversal was of the same magnitude after red or blue light even though the initial inhibiting effect of the two treatments differed.

A single 5 minute exposure to red followed by 55 minutes in darkness before the prolonged far-red treatment gave a smaller depression of anthocyanin formation than did two exposures to red, each followed by 55 minutes of darkness (Fig. 4). The effect of a single exposure to red was completely prevented by a subsequent brief far-red treatment, and the effect of two exposures was almost completely reversed; the slight loss of reversibility as the number of red/far-red cycles is increased

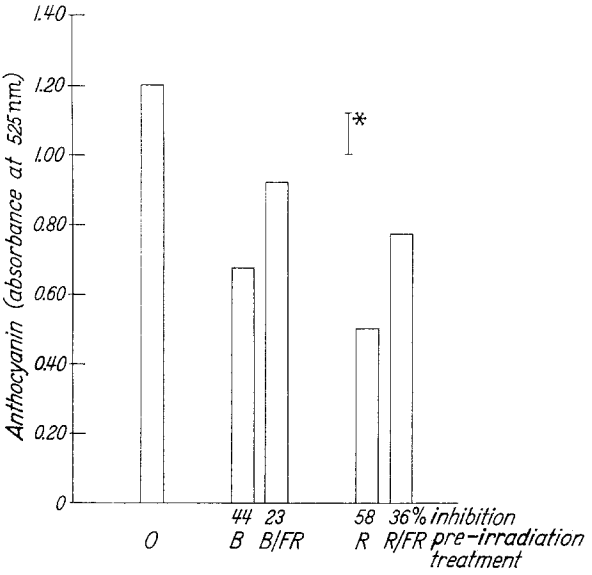

Fig. 3. The effect of intermittent pre-irradiation and its reversal by far-red. The six hour pre-irradiation treatments consisted of six 5-minute exposures to blue (*B*) or red (*R*) light, one at the beginning of each hour; after each light shot plants received 55 minutes darkness or 5 minutes far-red, 50 minutes dark (*FR*). The main light treatment consisted of 42 hours far-red. Seedlings were 48 hours old and were grown in phenylalanine at 25° C throughout. * Significant difference at $P = 0.05$

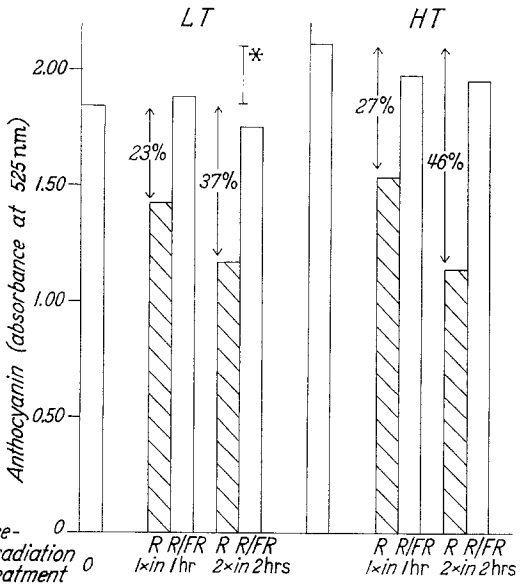

Fig. 4. The effect of short pre-irradiation treatments with red light and their reversal by far-red Seedlings were 57 hours old and grown in phenylalanine at 25° C throughout or pre-treated with high temperature (*HT*). The pre-irradiation treatments consisted of 5 minutes red/55 minutes dark (*R*) or 5 minutes red/5 minutes far-red/50 minutes dark (*R/FR*) given once or twice before transfer to 48 hours far-red. Control plants received 48 hours far-red. The intensity in red was 1.1 Kerg cm^{-2} sec^{-1}. * Significant difference at $P = 0.05$

(Figs. 3 and 4) is consistent with results obtained for other phytochrome responses such as flowering. A pre-treatment with high temperature, which was found to increase the responsiveness to the red/far-red reversible reaction of phytochrome after several hours in blue light, did not apparently affect the response studied here (Fig. 4).

Two five-minute exposures to red light given in two hours were as effective in depressing anthocyanin synthesis as a continuous exposure

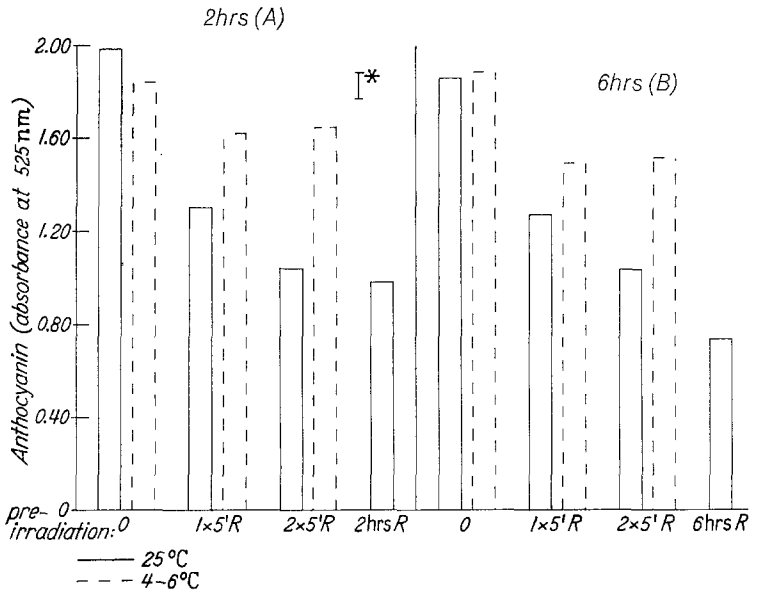

Fig. 5. The effect of temperature and duration of the dark period on the response to a pre-irradiation treatment with red light. During the two-hour and six-hour pre-treatments plants were given either 1×5 minutes red followed by 2 (*A*) or 6 (*B*) hours of darkness, or 2×5 minutes red at 1 hour intervals followed by 1 (*A*) or 5 (*B*) hours of darkness before transfer to far-red. All dark periods were given either at 25° C or 4—6° C. Treatments of two and six hours of continuous red light are included for comparison. The main light period consisted of 48 hours far-red. Seedlings were 60 hours old and grown in phenylalanine. The intensity in red was 3.9 Kergs cm^{-2} sec^{-1}. * Significant difference at $P = 0.05$

of two hours but were less effective than a continuous exposure to red for six hours (Fig. 5); six 5-minute shots of red were, however, as effective as six hours continuous light (Figs. 1 and 3). The magnitude of the effect thus depends primarily on the number of red shots given, one 5-minute shot every hour being fully as effective as continuous light. DE LINT and SPRUIT (1963) observed that, at an intensity of 2.5 Kergs cm^{-2} sec^{-1}, continuous irradiation with red for four hours destroyed only slightly more phytochrome than a single 10 minute exposure followed by four hours of darkness; for the pre-irradiation effect in turnip, however, a single exposure every hour is needed to equal the inhibiting effect of continuous light. As two 5-minute shots given in two hours is as effective

as two 5-minute shots given in six hours (Fig. 5) the rate of phytochrome destruction may be presumed to be so rapid that the P_{FR} formed by a single exposure to 5 minutes of red light is destroyed within about one hour. This presumed rate of destruction is faster than those observed spectrophotometrically in corn and pea. In corn mesocotyls at 27° C there is a 30 to 45 minute lag phase before destruction begins; no lag phase was observed in coleoptiles at this temperature but only about 50% of the P_{FR} was lost in one hour (BUTLER et al. 1963). In peas, at 25° C, there was no lag phase and 50—60% of the P_{FR} decayed in one hour (FURUYA and HILLMAN 1964). In both cases P_{FR} loss was complete in about 4 hours.

From measurements *in vivo* it has been shown that P_{FR} is relatively stable at low temperatures (DE LINT and SPRUIT 1963, FURUYA and HILLMAN 1964, BUTLER et al. 1963), whereas the photochemical conversion to P_{FR} takes place even in frozen samples (BUTLER et al. 1965). If P_{FR} destruction is prevented by low temperature during the dark periods following red light, transfer to far-red would almost immediately cause photochemical conversion to the stable P_R form and the rate of loss would decrease. The results of Fig. 5 are, therefore, also consistent with the hypothesis that phytochrome destruction following exposure to red light is the cause of the decreased anthocyanin synthesis in far-red, as the effect of red light was largely prevented when seedlings were kept at low temperatures (2—6° C) during the subsequent dark periods. The first exposure to red light had some effect, probably because a little time elapsed before the tissue reached the low temperature; a second exposure to red light then had no further effect. These results also suggest that phytochrome destruction begins very rapidly and with no lag phase.

Table 1. *Effect of nitrogen on the response to a pre-irradiation treatment with red light*

Seedlings were 60 hours old and grown in phenylalanine. The pre-treatment consisted of 2×5 minutes red in two hours; the main light treatment was 48 hours far-red. Nitrogen was given as a continuous flow throughout the pre-irradiation period, beginning 30 minutes before the first red exposure.

Pre-treatment	Main light	Anthocyanin content (absorbance at 525 nm)
None	Far-red	1.646 S.E. ±0.063
Red, air . . .	Far-red	0.991 ±0.042
Red, nitrogen	Far-red	1.434 ±0.035

P_{FR} decay is also considerably retarded at reduced oxygen concentrations though the photoconversions and dark reversion to P_R are not affected (BUTLER et al. 1965). The effect of pre-irradiation with red light in an atmosphere of nitrogen was, therefore, tested. Two exposures to 5 minutes red — 55 minutes dark were given in air or in nitrogen at 25° C. Nitrogen was removed by opening the boxes after the far-red irradiation had been given for about 20 minutes in order to ensure

complete reversion of P_{FR} before exposure to air. The results (Table 1) show that the depressing effect of the red pre-irradiations was largely prevented when they were given in an atmosphere of nitrogen.

In the final experiment a dark period of one hour after the second exposure to red light was compared with one of 13 hours. The amount of anthocyanin formed in the pre-irradiated seedlings was independent

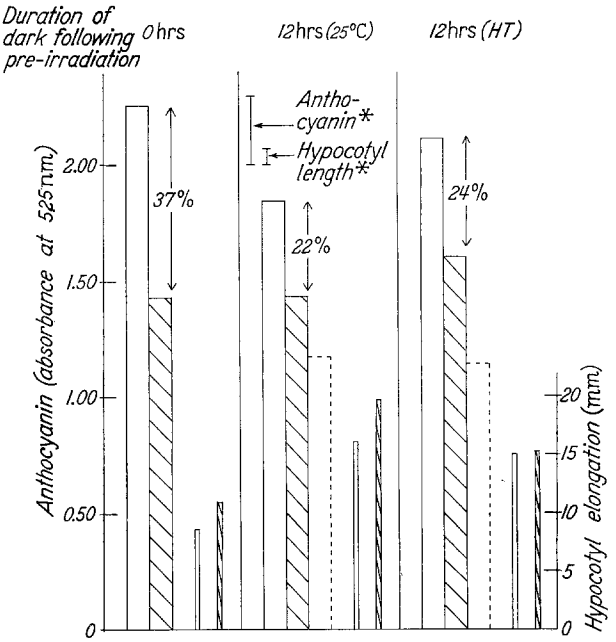

Fig. 6. The effect of duration of the dark period on the response to a pre-irradiation treatment with red light. The pre-irradiation consisted of 5 minutes red/55 minutes dark given twice before transfer to 48 hours far-red immediately (*0*) or after a further 12 hours of darkness (12) at 25° C or 35° C. The control plants (open bars) received 48 hours of far-red without pre-irradiation. The dotted lines indicate the amount formed when the pre-irradiation was given immediately before the far-red treatment, i.e. at the end of the 12 hour dark period. Seedlings were 46 hours old and grown in phenylalanine. The intensity in red was 1.1 Kerg cm^{-2} sec^{-1}. * Significant difference at $P = 0.05$

of the length of the dark period (Fig. 6) but, as the anthocyanin content of the control plants was decreased because of ageing, the percentage depression was slightly less with the 13 hour dark period. An immediate pre-irradiation of plants of the same age resulted in a greater depression than the one given 13 hours earlier, suggesting that some *de novo* synthesis of phytochrome may have occurred during the long dark period.

It is interesting that the pre-irradiation treatments with red light also reduced the effect of prolonged irradiation with far-red on hypocotyl elongation and that this red effect is also reversed by a brief far-red exposure (Table 2). Again a pre-irradiation treatment with red light did not affect the response to blue light. This raises the question of how

Table 2. *Effect of a pre-irradiation treatment with red and far-red on the response of hypocotyls to prolonged irradiation with far-red or blue light*

Pre-treatment	Main light hrs.	Hypocotyl length mm	
		in phenylalanine	in water
None	42 far-red	16.9	
6 × 5′ red/55′ dark. . . .	42 far-red	19.0	
6 × 5′ red/5′ FR/50′ dark	42 far-red	16.3	
None	42 blue	18.1	
6 × 5′ red/55′ dark. . . .	42 blue	16.2	
		S.E. mean ± 0.46	
None	48 far-red	10.8	11.2
6 hrs. red	42 far-red	15.7	18.1
None	48 blue	13.3	15.1
6 hrs. red.	42 blue	13.9	16.1
None	48 red	19.6	20.6
		S.E. mean ± 0.44	S.E. mean ± 0.67
Dark	Dark	31.73	
		S.E. mean ± 0.99	

closely the two processes of growth and anthocyanin synthesis are linked; the pre-irradiation with red did not reduce the growth response to far-red when plants were kept in darkness at high temperature for 13 hours before the far-red treatment, although the effect on anthocyanin synthesis still remained (Fig. 6).

IV. Discussion

The depressing effect of a pre-irradiation with red light on subsequent anthocyanin synthesis in prolonged far-red is clearly dependent on phytochrome as it is reversible by brief exposures to far-red and also occurs when intermittent brief shots of red light are given. It is not simply that anthocyanin synthesis in prolonged far-red light is inhibited by the presence of P_{FR}, because most of the P_{FR} formed in response to red and not destroyed would be immediately converted to P_R on transfer to far-red. Phytochrome destruction following conversion to the P_{FR} form by red light is, therefore, the most likely explanation of the effect. A very rapid inhibiting effect catalysed by P_{FR} cannot be entirely ruled out, but the increase in anthocyanin synthesis brought about by a brief exposure to red after several hours of blue light (GRILL 1965) would then be hard to explain. The reults using low temperatures and an atmosphere of nitrogen are consistent with the suggestion that phytochrome destruction is involved but would also be observed with a P_{FR} — catalysed oxidative thermal inhibition.

In these experiments a pre-irradiation with blue appears to be almost as effective as red light when given continuously or intermittently in

5-minute shots. Rates of phytochrome destruction in blue light have not been determined but may be estimated from the destruction rates at other wave-lengths. BUTLER et al. (1963) and BUTLER (1964) have shown that in corn the rate of phytochrome decay is dependent on the proportion in the P_{FR} form up to 10% P_{FR}; above this the rate of decay is in dependent of the amount in the P_{FR} form. In blue light at photo-equilibrium 35—50% of the phytochrome is present as P_{FR} (BUTLER et al. 1964) so the rate of decay should be similar to that in red light. The depressing effects of pre-irradiation treatments with red and blue may thus both be attributed to phytochrome destruction in the tissue following conversion to P_{FR}.

A depressing effect of red light on the response to far-red irradiation has also been observed on the elongation of Avena coleoptiles (AGHION 1962) and on oxygen uptake in *Sinapis alba* (HOCK and MOHR 1964) but a similar explanation was not offered.

Pigment formation in blue light was not affected by a pre-treatment with red. At first sight this suggests that the blue and far-red peaks of the high-energy reaction operate through different photoreceptors as a pre-irradiation, here equated with "phytochrome destruction", markedly depresses pigment formation in far-red. However, the results show that the "phytochrome destruction" effect occurs very rapidly and that blue light is almost as effective as red in causing it. Consequently the effect of prolonged blue irradiation can never be observed without concomitant "phytochrome destruction". In blue light, therefore, we observe a response to prolonged irradiation that is not dependent on the presence of destructible phytochrome in the same way as it is in far-red.

Several questions still remain unanswered; the first is whether all of the effects of prolonged far-red light in turnip are mediated through phytochrome or whether a "high energy" far-red reaction is also involved. At present it is not possible to answer this question. Even when six hours of red light were given before transfer to far-red anthocyanin synthesis was depressed by only 60% and the yield was about the same as in blue light; however, it cannot be assumed that such a treatment would totally destroy phytochrome as plants are sensitive to low energies of red and far-red after many hours of illumination, and phytochrome has been shown to be present at low concentrations in a number of mature green plants (LANE et al. 1963). The amount remaining may be sufficient to bring about anthocyanin synthesis when prolonged far-red is given: it is also possible that some new synthesis occurs.

The second question is why, if far-red acts by keeping a low level of P_{FR} in the tissue due to the far-red absorption tail of P_R as suggested by BUTLER et al. (1963), continuous red light is not as effective as far-red in promoting anthocyanin synthesis and inhibiting elongation. It is

possible that in turnip phytochrome destruction occurs so rapidly in red light (due to the formation of large amounts of P_{FR}) that the reactions catalysed by P_{FR} cannot take place; far-red light, on the other hand, would cause the formation of small quantities of P_{FR} over an extended period and this might be more effectively utilised. The experiments with intermittent irradiation suggest that the rate of phytochrome destruction in turnip is faster than that found in pea or corn.

BUTLER and LANE (1965) have raised the question of whether there is any physiological or chemical difference between the phytochrome that is present in large quantities in etiolated tissue and is destroyed by light and the small fraction that remains active even in continuous light. The photo-labile phytochrome appears to play an important role in anthocyanin synthesis in response to far-red light in turnip. The reversible red/far-red reaction of phytochrome also operates in the control of anthocyanin synthesis even after several hours of blue light (GRILL 1965) so that some phytochrome still remains and influences anthocyanin formation even after prolonged exposures to light.

An interesting question is why some other plants do not respond to far-red irradiation even though the dark-grown seedlings have a high phytochrome content; dark-grown sunflower seedlings, for example, are a rich source of phytochrome (BUTLER et al. 1965) but prolonged far-red does not cause anthocyanin synthesis; only the red/far-red reversible reaction of phytochrome and a response to prolonged blue irradiation can be observed (unpublished results).

The interpretation of the results of these experiments has been that enzymatic destruction of phytochrome following conversion to P_{FR} causes the decreased photosensitivity to prolonged far-red irradiation; it should be emphasised that this assumption is based only on physiological experiments and direct spectrophotometric measurements of the phytochrome concentrations in the tissue are needed. Furthermore little is known of the process of phytochrome decay following red light; it has been suggested that decay may actually represent change to a growth active but optically undetectable form (HILLMAN 1964), but our results imply that destruction of phytochrome results in loss of some of its physiological effect.

Zusammenfassung

Die Anthocyanbildung war im langfristig gegebenen Dunkelrot bis zu etwa 60% reduziert, wenn die ersten 6 Std durch hellrote oder blaue Bestrahlung ersetzt wurden; Hellrot oder Dunkelrot in gleicher Weise im Dauerblaulicht substituiert waren praktisch wirkungslos. Daraus wird geschlossen, daß der Effekt einer Dauerbestrahlung mit Blau und Dunkel-

rot, zum Teil jedenfalls, auf verschiedene Photorezeptoren zurückzuführen ist.

Der Effekt einer Vorbehandlung mit hellrotem oder blauem Licht trat auch dann auf, wenn nur kurzfristige Bestrahlungen gegeben wurden und konnte durch unmittelbar nachfolgende kurze Dunkelrot-Belichtung wieder aufgehoben werden. Die Hemmung durch kurzfristige Vorbestrahlung konnte weitgehend verhindert werden, wenn die Keimlinge während der Dunkelperiode, vor der Übertragung in Dauerdunkelrot, bei tiefer Temperatur oder unter Stickstoff gehalten wurden. Der Vorbelichtungseffekt wird auf die enzymatische Destruktion von Phytochrom, nach der Umwandlung in die P_{FR}-Form, zurückgeführt und es wird vermutet, daß die Anthocyansynthese im Dauerdunkelrot weitgehend phytochromabhängig ist, wahrscheinlich durch die Aufrechterhaltung eines niedrigen P_{FR} Niveaus im Gewebe infolge der schwachen Absorption von P_R im Dunkelrot.

Eine Vorbelichtung mit Hellrot verringerte ebenfalls die hemmende Wirkung von Dunkelrot auf das Hypokotylwachstum, war jedoch ohne Einfluß im Blaulicht.

This work was supported by a grant of the Agricultural Research Council.

Literature

AGHION, Y., C. YOUGLARD et A. LOURTIOUX: Effets d'éclairements colorés de faibles énergies sur la croissance de coléoptiles d'avoines in vitro. Physiol. Plantarum (Kbh.) **15**, 452—456 (1962).

BUTLER, W.L.: Symposium on photomorphogenesis in plants. II. Dark transformations of phytochrome in vivo. Quart. Rev. Biol. **39**, 6—10 (1964).

— S.B. HENDRICKS, and H.W. SIEGELMAN: Action spectra of phytochrome in vitro. Photochem. and Photobiol. **3**, 521—528 (1964).

— — — Purification and properties of phytochrome. In: Chemistry and biochemistry of plant pigments (Ed. T.W. GOODWIN). London-New York: Academic Press 1965.

—, and H.C. LANE: Dark transformations of phytochrome in vivo. II. Plant Physiol. **40**, 13—17 (1965).

— — and H.W. SIEGELMAN: Nonphotochemical transformations of phytochrome in vivo. Plant Physiol. **38**, 514—519 (1963).

FURUYA, M., and W.S. HILLMAN: Observations on spectrophotometrically assayable phytochrome in vivo in etiolated pisum seedlings. Planta (Berl.) **63**, 31—42 (1964).

GRILL, R.: Photocontrol of anthocyanin formation in turnip seedlings. 1. Demonstration of phytochrome action. Planta (Berl.) (in Press).

HEATH, O.V.S., and D. VINCE: Some non-photosynthetic effects of light on higher plants with special reference to wave-length. Symp. Soc. exp. Biol. **16**, 110—137 (1963).

HENDRICKS, S.B.: Control of plant growth by phytochrome. In: Comparative effects of radiation (Eds. M. BURTON, J.W. KIRBY-SMITH and J.L. MCGEE). New York-London: John Wiley & Sons 1960.

HILLMAN, W.S.: Phytochrome levels detectable by in vivo spectrophotometry in plant parts grown or stored in the light. Amer. J. Bot. **51**, 1102—1107 (1964).

Hock, B., and H. Mohr: Die Regulation der O_2-Aufnahme von Senfkeimlingen (*Sinapis alba L.*) durch Licht. Planta (Berl.) **61**, 209—228 (1964).

Lane, H.C., H.W. Siegelman, W.L. Butler, and E.M. Firer: Detection of phytochrome in green plants. Plant Physiol. **38**, 414—416 (1963).

Lint, P.J.A.L. de, and C.J.P. Spruit: Phytochrome destruction following illumination of mesocotyls of *Zea Mays L.* Meded. Landbouwhogeschool. Wageningen **63**, 1—7 (1963).

Mohr, H.: The control of plant growth and development by light. Biol. Rev. **39**, 87—112 (1964).

Sale, P.J.M., D. Vince, and J.E. Prue: Kinetics of the photo-inhibition of stem growth in *Pisum sativum* and *Tropaeolum majus*. Photochem. and Photobiol. **3**, 61—65 (1964).

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

Vince, D.: Photomorphogenesis in plant stems. Biol. Rev. **39**, 506—536 (1964).

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