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REQUIREMENTS OF BLUE, UV-A, AND UV-B LIGHT FOR NORMAL GROWTH OF HIGHER PLANTS, AS ASSESSED BY ACTION SPECTRA FOR GROWTH AND RELATED PHENOMENA

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INTRODUCTION

It is very important for experimental purposes, as well as for the practical use of plants when not enough sunlight is available. To grow green higher plants in their normal forms under articicial lighting constructing efficient and economically reasonable lighting systems is not an easy task. One possible approach would be to simulate sunlight in intensity and the radiation spectrum, but its high construction and running costs are not likely to allow its use in practice. Sunlight may be excessive in irradiance in some or all portions of the spectrum. Reducing irradiance and removing unnecessary wavebands might lead to an economically feasible light source. However, removing or reducing a particular waveband from sunlight for testing is not easy. Another approach might be to find the wavebands required for respective aspects of plant growth and to combine them in a proper ratio and intensity. The latter approach seems more practical and economical, and the aim of this Workshop lies in advancing this approach. I summarize our present knowledge on the waveband requirements of higher plants for the regions of blue, UV-A and UV-B.

BLUE LIGHT (BL)

The significance of this waveband was first noticed in phototropism, a response to light direction in which shaded and illuminated plant organs grow at different rates, resulting in curvature towards or away from a light source (Iino, 1990). Although red light, mediated through phytochrome, can induce phototropic responses under special circumstances (Parker et al., 1989), it seems probable that specific BL photoreceptors play a prominent role in most light-oriented growth movements as well as in many photoregulated, turgor-driven responses, such as nastic movements, leaf solar tracking (Koller, 1990) and stomatal opening (Zeiger, 1983). Plant movements have been popular objects of study because they occur rapidly and in many cases are reversible. Nonetheless, in spite of much exquisite physiology, it has not yet been possible to identify positively and BL photoreceptors involved in these responses. This is not surprising, given the likelihood that such photoreceptors are present in low abundance as well as the number of overlapping chromophores in this portion of the spectrum. Flavoproteins are probable candidates for BL photoreceptors (Short and Briggs, 1994). Recent evidence obtained with a mutant of *Arabidopsis* suggests that a putative BL photoreceptor associated with hypocotyl elongation may be closely related to a flavoprotein enzyme responsible for light-mediated repair of cyclobutane phyrimidine dimers in DNA (Ahmad and Cashmore, 1993). Still, other studies continue to support the possibility that pterins (Galland and Senger, 1988) or carotenoids (Quiñones and Zeiger, 1994) play a role in

some BL responses.

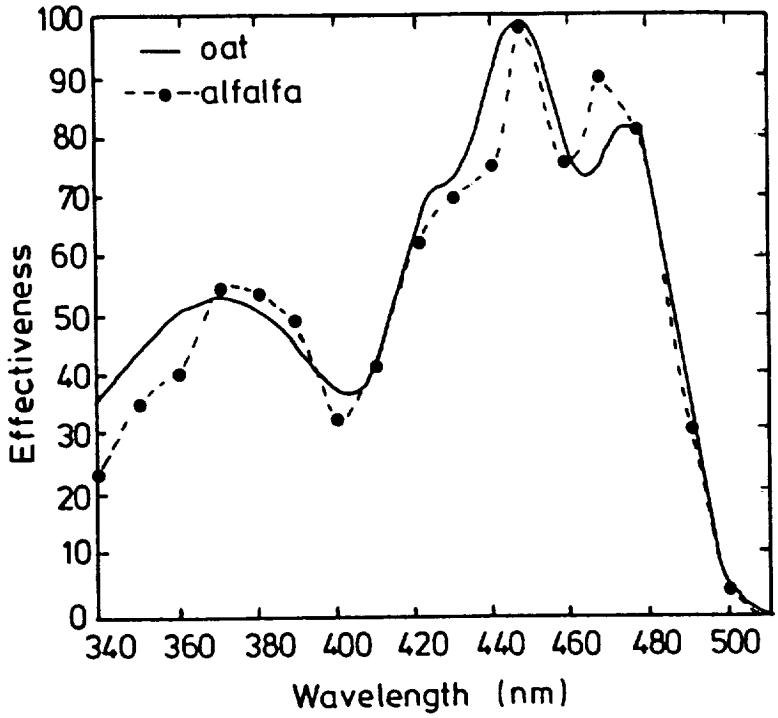

Fig. 1. Action spectra for first-positive phototropic curvature in the oat coleoptile and alfalfa hypocotyl. (Adapted from Thimann and Curry 1960, Baskin and Iino 1987).

Assessing the contribution of BL photoreceptors in a white light environment is complicated by numerous reports that the activity of BL phtoreceptors is influenced by additional photoreceptors absorbing in other spectral bands. For example, red light counteracts BL-induced photoepinastic orientation of rice and wheat leaves but has no effect by itself (Table 1; Inada, 1969; Kimura, 1977). This interaction is presumed to underlie the intermediate nastic response observed under white light. Phytochrome may be involved in many interactions with BL photoreceptors. In fact, formation of Pfr either before or immediately after a BL pulse suppressed the BL-induced unrolling of etiolated rice leaves (Sasakawa and Yamamoto, 1980). However, long wavelength suppression of BL-induced tea leaf orientation activity peaked at 600 nm, while wavelengths of 620 nm or longer were inactive (Aoki et al., 1981).

TABLE 1. Photoepinasty of the 2nd leaf of intact rice seedlings, cv. T 136

Light treatments	Leaf blade angle (degree)
Dark control	2.9 ± 3.5
Blue	67.5 ± 14.1
Red	4.6 ± 5.5
White	14.6 ± 5.0

11 W $m^{-2}s^{-1}$ PAR for 3 days, + S.D. (n = 20) (Inada, 1969)

TABLE 2. Light induced unrolling of the 2nd leaf intact rice seedlings, cv. Norin No. 25

Light treatments	Diameter of rolled leaf (mm ± S.D.)
Dark control	0.40 ± 0.07
Blue	2.08 ± 0.17
Green	0.71 ± 0.20
Red	0.78 ± 0.13
White	1.53 ± 0.40

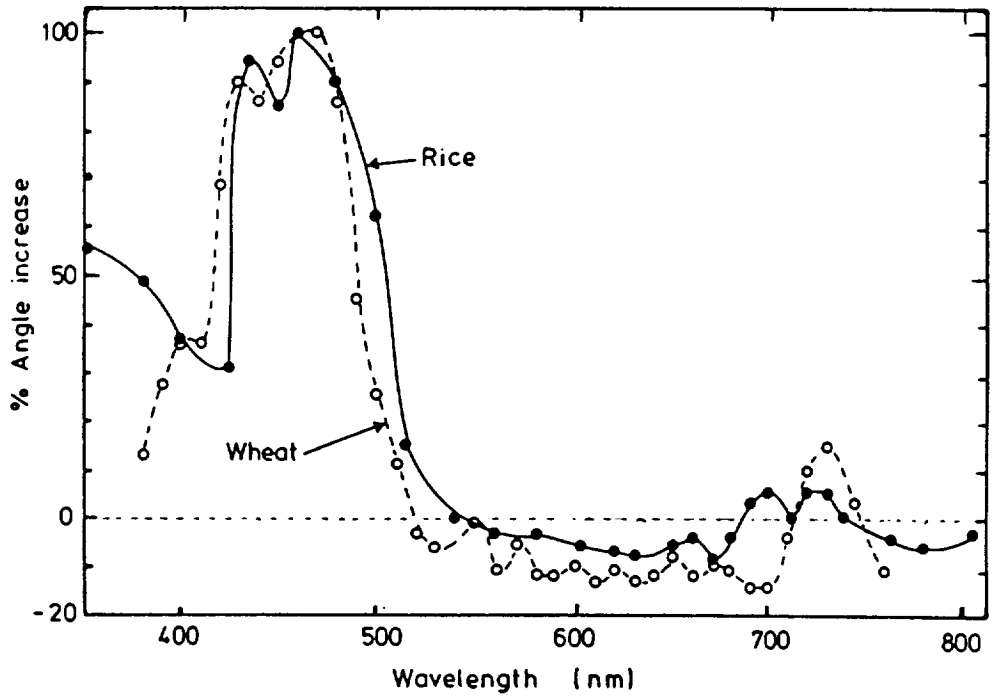

Fig. 2. Response spectra for photonastic inclination of rice and wheat leaf blades (from Inada, 1969 and Kimura, 1974). For rice and wheat, respectively, irradiation, 3 W m^{-2} x 72 h and 0.625 W m^{-2} x 40 h; leaf blade angles of non-irradiated control, 2° and 20°; light-induced maximum increases in angle (100%), 26° and 25°.

Blue light-induced growth inhibition of the stem is a phenomenon distinct from the phototropism of the stem, although the curvature involves a growth inhibition of the lighted side and a growth promotion of the shaded side of the stem. While a phototropic curvature appears approximately 30 minutes after the onset of light, stem growth inhibition occurs in some minutes (Fig. 3). Further, it was found that a phototropically null mutant of *Arabidopsis* showed normal hypocotyl growth inhibition, while another mutant lacking growth inhibition showed normal phototropic response (Liscum et al. 1992). Although the so-called high irradiance response (HIR) has been suggested to be responsible for BL effect as well (Wildermann et al. 1978), and may occur in the seedling stage, there certainly exist

BL-specific actions, which are separable from phytochrome actions by faster appearance and disappearance of growth inhibition after a pulse (Fig. 3) (Gaba and Black 1979, Behringer and Davies 1993). This was also shown by phytochrome-deficient mutant seedlings of *Arabidopsis* (Chory 1993, Goto et al. 1993). An action spectrum for the hypocotyl growth inhibition of the mutant completely lacks action at above 500 nm, while that for a wild type has peaks which suggest an occurrence of a low photon response and HIR of phytochrome (Fig. 4). In the *aurea* tomato mutant the accumulation of transcripts from nuclear genes for thylakoid proteins requires BL even when saturated with RL (Palomares et al. 1991).

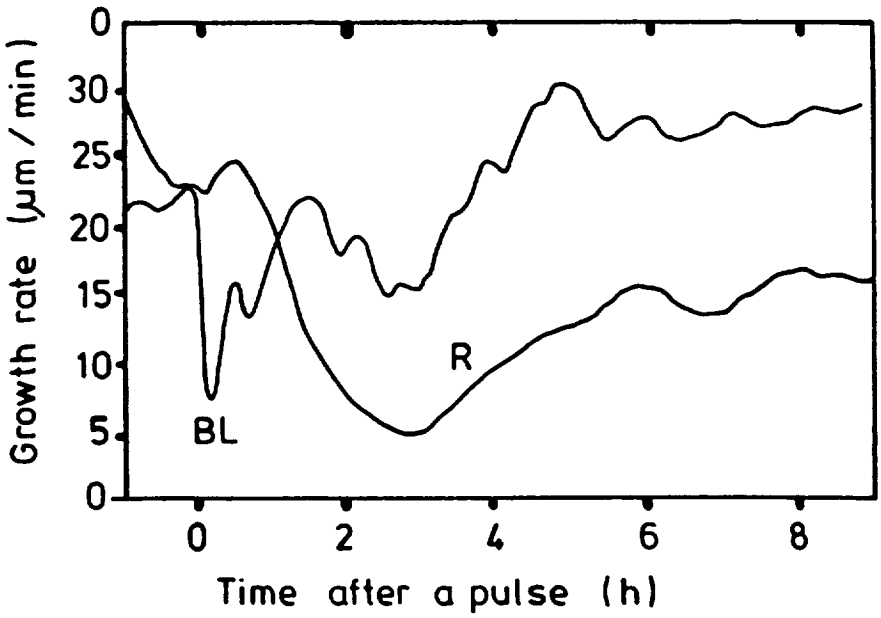

Fig. 3. Early time course of the light growth inhibition of etiolated pea seedlings. (Adapted from Behringer and Davies 1993).

In considering light sources for photoautotrophic growth of plants, our interest is to what extent BL influences plant growth in the background of sufficient photosynthetically active radiation (PAR). Some attempts to see the effects of BL in sunlight have been made. From sunlight or intense white light from "Youkou Lamps" (DR400T, Toshiba, Tokyo) in a phytotron the BL waveband was removed or reduced in intensity by filtering with yellowish polyacrylic resin or polyvinyl chloride sheet (Nakamura et al. 1977, Yamada et al. 1977). The results showed increased growth of the stem and petiole in Japanese honeywort, celery and bean, and a curling of the leaf blade in celery. But in these experiments UV-A and -B were along with BL removed, but it was not indicated whether UV-A and -B were removed in the control as well; thus it is unclear whether or not these are BL-specific action.

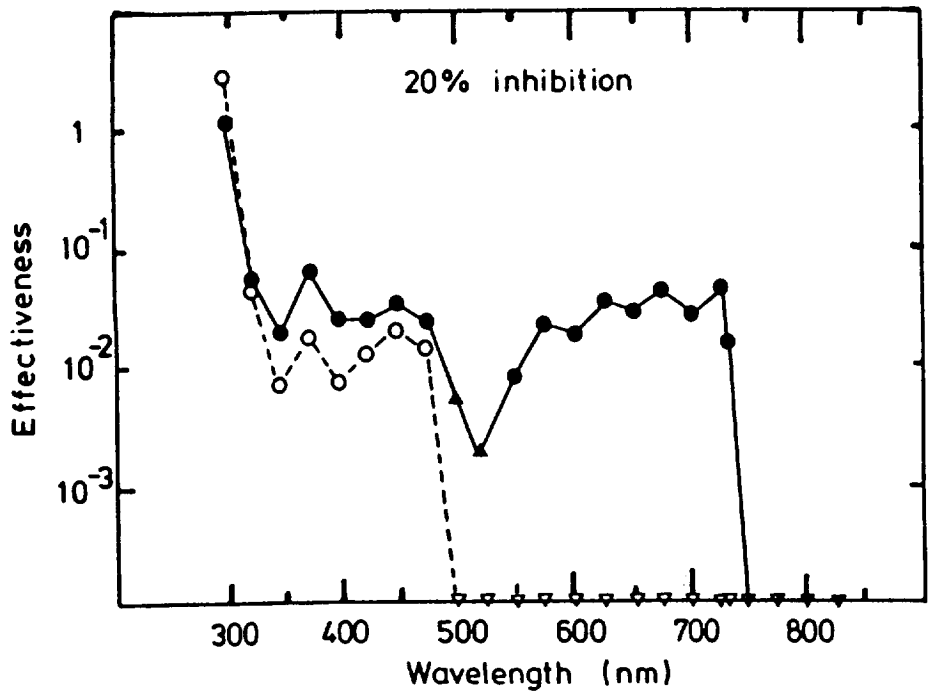

Fig. 4. Action spectra for the light growth inhibition of the hypocotyl in wild-type (solid line) and phytochrome-deficient mutant (*hy2*) (broken line) of *Arabidospsis thaliana*. (From Goto et al. 1993).

In another line of experiments (Inada and Katsura 1977), rice, soybean, tomato, and cucumber were grown for 38 days under WL from "Youkou Lamps" with or without a small BL supplement (Fig. 5). Extra BL caused significant photomorphogenetic effects (e.g. suppression of shoot extension in soybean and rice (Table 3) and increase of stem thickness. In tomato, general growth was promoted as shown by an increase of dry weight, while no apparent suppression in plant height was observed.

These results show BL has specific morphogenetic effects. The BL actions are on balance with OL or RL, and even under intense WL from metal halide lamps or likes, BL supplement is required.

UV-A LIGHT

Many action spectra with their main peak in the blue region (ca. 450 nm) have a subpeak in the UV-A region (ca. 370 nm), and both peaks are assumed to be due to the same photoreceptor, for which the name blue-near UV photoreceptor or cryptochrome has been coined. Such a UV-A requirement may be satisfied by BL. However, there are some other UV-A requirements which are not replaced by BL. In a frame covered with a polyvinyl chloride sheet to cut off UV of wavelengths below 400 nm, spinach grew better than in a control frame covered with UV-transparent sheet (Hasegawa et al. 1979), suggesting a general growth inhibition by the solar UV. Installment of a UV-A source (black light) in the former frame (solar UV-A eliminated), however, increased the growth of spinach (Shibata 1993), whereas an inclusion of a UV-B source inhibited growth. In a similar experiment with polyvinyl sheet frames deprived of solar UV, by contrast, tomato and radish plants grew less than in control frames with solar UV transmitted (Tezuka et al. 1993). The contrasting

results with the solar UV elimination between Hasegawa et al's and Tezuka et al's experiments seem due to the different sensitivities to UV-A or UV-B of the particular plants studied. Since in the UV elimination experiments described above as well as the experiment with a UV supplement to white light, sufficient amounts of BL and RL are supplied from sunlight, the results may suggest the occurrence of UV-A specific action. The construction of an action spectrum of UV-A in the presence of intense white light is required.

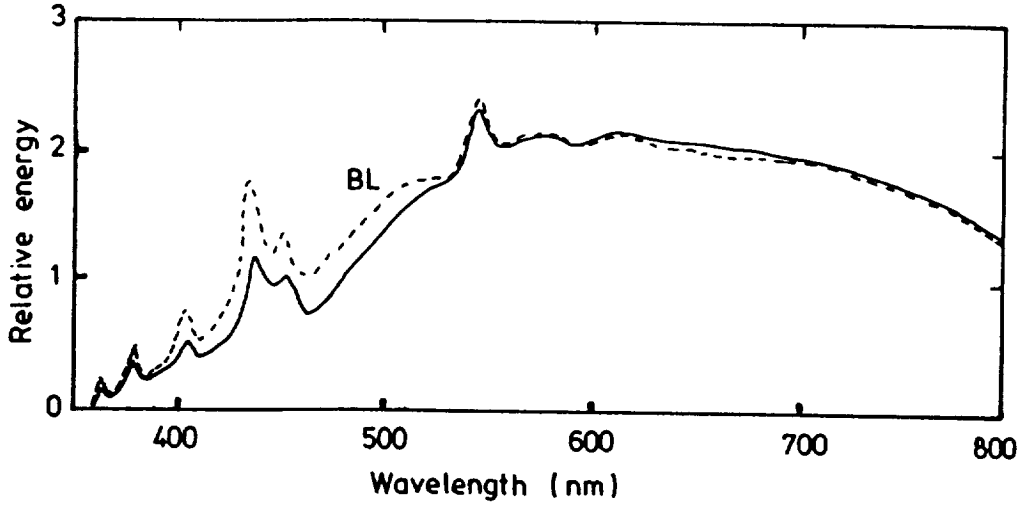

Fig. 5. Spectral energy distribution of the main light source (Youkou Lamps, 400 watts, Toshiba, Tokyo) (solid line) and of the light supplemented with BL from fluorescent tubes (broken line). The colour temperatures: 4000 K and 4500 K, respectively. (from Inada and Katsura 1977).

Photoreactivation of UV damage is an important action not to be neglected in this spectral region. However, few action spectra have been determined with living higher plants. Figure 6 shows action spectra for photoreactivation determined with enzymes isolated from plant tissues, and indicates the necessity of light of this waveband in relation to UV-B.

TABLE 3. Effects on plant morphogenesis of BL supplemented to white light "Toshiba Youkou Lamps"

Plants	Plant height (%)	Dry weight (%)	DW/height (%)
Rice	92**	99	108
Soybean	84**	106	126
Tomato	104	138*	133
Cucumber	87	98	113

White light control = 100%, * and ** denote significant differences at 5% and 1% levels, respectively. White light without BL supplement, 230 W m^{-2}. Day: 15h, 25°C; night: 9h, 20°C. 38 days culture. (Inada and Katsura, 1977).

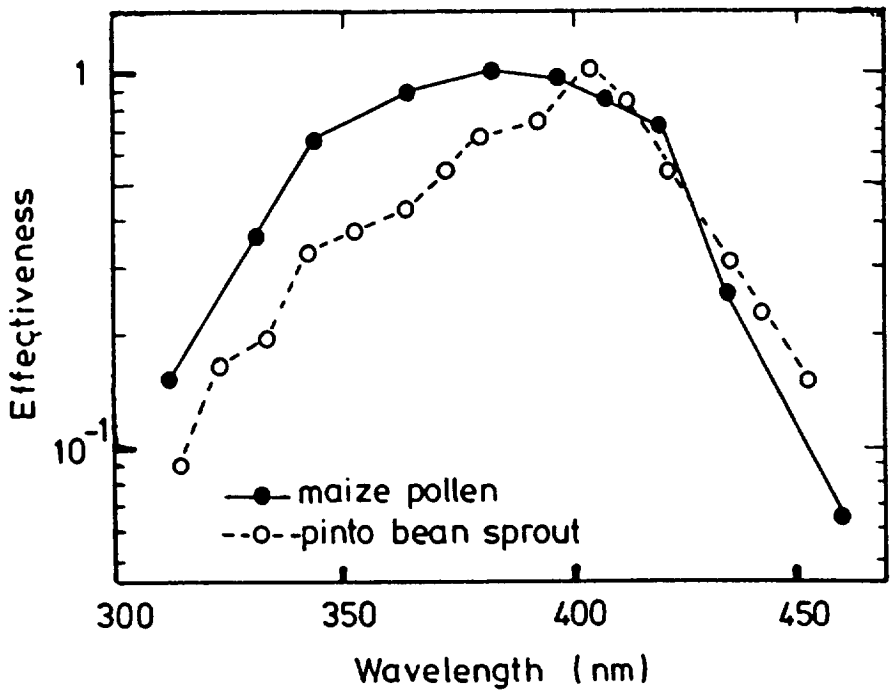

Fig. 6. Action spectra for photoreactivating enzymes isolated from Pinto bean sprouts (Saito and Werbin 1969) and maize pollen (Ikenaga et al. 1974).

UV-B LIGHT

This waveband exerts various actions: suppression of the over-all growth of plants, reducing cell division or elongation; cell damage such as cell collapse and tissue browning; and reduction of biomass production (Caldwell 1971, Tevini and Teramura 1989). Besides, this waveband causes photomorphogenesis, and induces the synthesis of anthocyanin and other flavonoids alone or in coaction with RL absorbed by phytochrome (Beggs et al. 1986). In intact plants flavonoids are synthesized in the epidermis, and serve as a UV-B cut-off filter to the light entering the tissue (Schmelzer et al. 1988, Tevini et al. 1991, Cen and Bornman 1993).

The flavonoid-inducing effect of this waveband is established by action spectra (Fig. 7). They have peaks at ca. 290 nm, differing from the absorption of DNA or RNA, and suggest the occurrence of a particular UV-B photoreceptor. This UV-B action is manifested or enhanced by phytochrome action (Yatsuhashi and Hashimoto 1985), and further enhanced by BL (Drumm and Mohr 1978, Duell-Pfaff and Wellmann 1982). That the flavonoid induction by UV-B really occurs in the natural growing conditions was shown by the effects of UV-B supplements to artificial WL (Adamse and Britz 1992, Arakawa et al. 1985, Maekawa et al. 1980, Cen and Bornman 990) and supplement to sunlight (Flint et al. 1985). The findings that UV-B elimination from sunlight greatly reduced anthocyanin synthesis in rose flowers and eggplant fruits (Mihara et al. 1973, Tezuka et al. 1993) support the view that the solar UV-B produces flavonoid synthesis under the field conditions. Lignin biosynthesis, whose early steps (phenylpropanoid pathway) are shared with flavonoid synthesis, may be under the influence of UV-B, since UV-B makes plants tougher (Hashimoto and Tajima 1980).

When given at a moderate intensity together with sufficient photosynthetically active radiation (PAR), UV-B increases the thickness of the leaf (Cen and Bornman 1990, 1993) and chlorophyll content (Adamse and Britz 1992, Hashimoto and Tajima 1980), and does not suppress photosynthesis (Adamse and Britz 1992, Bornman 1989, Flint et al. 1985) except for sensitive species, strains or varieties. Suppressed growth of the hypocotyl and promoted expansion of the leaf or cotyledons are characteristics of morphogenetic effects of light. UV-B suppresses the growth of the hypocotyl of cucumber, eggplant and radish (Ballare et al. 1991, Hashimoto and Tajima 1980) without causing growth inhibition of the cotyledons. The findings with light-grown cucumber that the cotyledons perceive light and the hypocotyl responds (Ballare et al. 1991) strongly suggest that it is a normal photomorphogenetic action of UV-B. In this UV-B action a small photon leved of UV-B is enough. Wavelengths over 300 nm may be effective. Kondo (Hashimoto et al. 1993) found that an addition of 310 nm light at 0.1 to 1 μmol m^{-2} s^{-1} promoted the growth of cucumber first leaf under intense white light (500 μmol m^{-2} s^{-1}), while 290 nm light at the same photon levels showed neither promotion nor inhibition. Each wavelength was inhibitory when given alone. Although no action spectrum is available yet for either hypocotyl inhibition or cotyledon promotion, the promotive effect of 310 nm distinguishes the effect of the longer wavelength region of UV-B from the general growth inhibitory effects of UV-B. Thus, UV-B is assumed to exert true photomorphogenetic actions in addtion to the deleterious effects. This view has been proposed by Hashimoto and Tajima (1980), Ballare et al.(1992), and Ensminger (1993).

However, it is indeed true that UV-B causes damage in plants. The action spectra for the formation of pyrimidine dimers and (6-4)photoproduct, as examined with a human cell culture or calf thymus DNA solution, peak at about 260 nm and extend their longer wavelength ends into the UV-B region (Matsunaga et al. 1991, Rosenstein and Mitchell 1987), and it is assumed that this is also the case with plants. Coiling, a UV-B-induced abnormal growth of the etiolated sorghum first internode (Fig. 8), closely correlates with the amount of thymine dimer formed by the irradiation (Tsurumi et al. unpublished data), and the action spectrum for coiling corresponds with the absorbance of DNA. An action spectrum for anthocyanin synthesis inhibition shows a similar curve (Fig. 8) (Hashimoto et al. 1991, Wellmann et al. 1984).

Thus, the UV-B region is the crossing zone of the deleterious effects and the normal photomorphogenetic actions, as indicated by the distinct action spectra (Figs. 7, 8). The photon level of UV-B required for the photomorphogenetic actions is lower than for the deleterious effects of UV-B (Fig. 9). The photon ratios (curve A/curve B) required for threshold induction are estimated from Fig. 9 as 1/380, 1/1400, and 1/6500, respectively, at 280, 290, and 297 nm. The trend of the values implies that at above 300 nm the deleterious effects of UV-B are not likely to occur at the photon levels required for the photomorphogenetic effects of UV-B. The presence of sufficient PAR and carbon dioxide ameliolate the harmful effects of UV-B (Adamse and Britz 1992, Cen and Bornman 1990, Nouchi 1993, Teramura et al. 1980). The amelioration of UV-B damage by PAR involves photoreactivation by UV-A and BL and other unknown action mechaninsms of visible light in addition to an increase of the biochemical UV-B filter flavonoids. Thus, to obtain the beneficial effects of UV-B and minimizing potential harmful effects, a long-wavelength UV-B

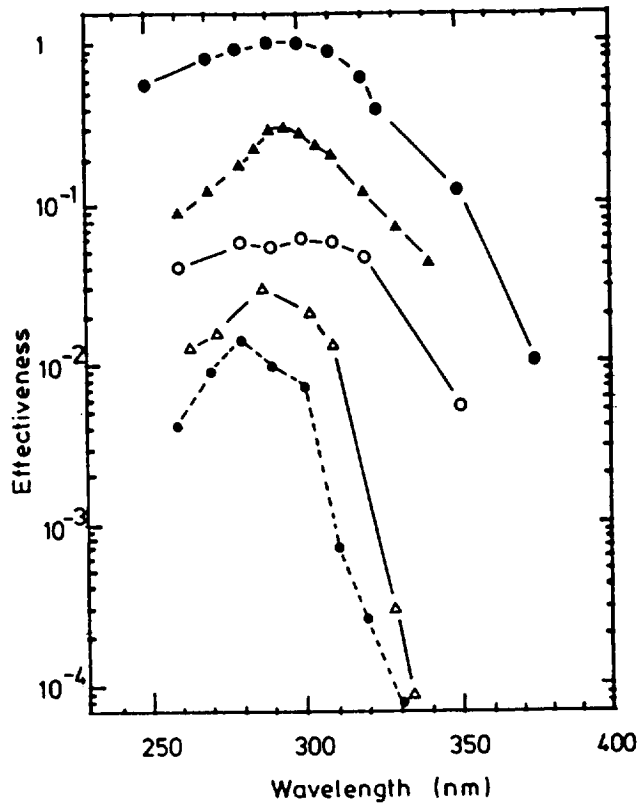

Fig. 7. Action spectra for flavonoid synthesis induction in Spirodela; --●--, anthocyanins; (Ng et al. 1964), parsley --▲--, flavon glycosides; (Wellmann 1975), maize --○--, anthocyanins; (Beggs and Wellmann 1985), sorghum --△--, anthocyanins; (Yatsuhashi et al. 1982), and carrot cell culture --●--, anthocyanins; (Takeda and Abe 1992). (Adapted from Ensminger 1993).

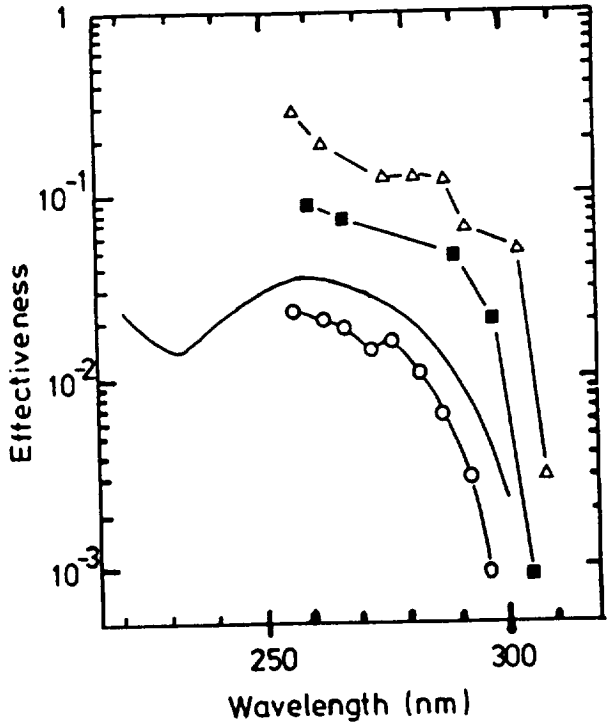

Fig. 8. Action spectra for mesocotyl coiling in sorghum (△) ,(Hashimoto et al. 1984), root growth inhibition in cress (■) , (Steimetz and Wellmann 1986), and anthocyanin induction inhibition in sorghum (○), (Hashimoto et al. 1991), and the absorption spectrum of DNA (solid line).

source should be installed at small UV-B/PAR ratios.

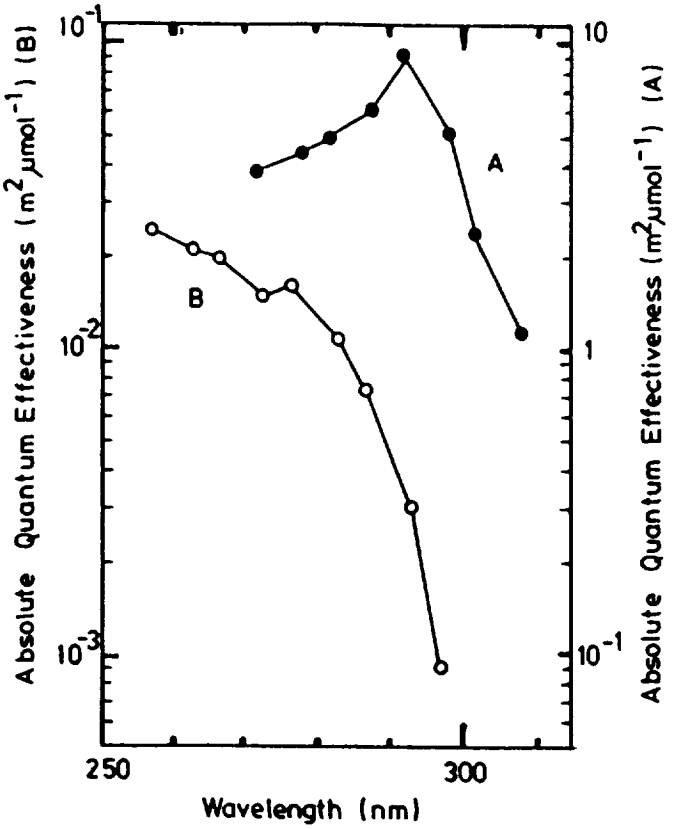

Fig. 9. Distinct effective waveband and different photon effectiveness between the photomorphogenetic actions and deleterious effects of UV-B, as represencted by anthocyanin induction (A) and inhibition (B). (Adapted from Hashimoto et al. 1991).

Since higher plants have developed their present characteristics under sunlight during the long process of evolution, it is quite natural that they adapted themselves to the present state of light environment. Higher plants seem to require all the spectrum bands, except for the band wavelengths 800 nm, of the sunlight coming on the Earth's surface. Blue, UV-A and UV-B light have their respective specific photomorphogenetic actions for higher plants, and are not replaced by light of other wavebands. These wavebands of radiation cooperate (UV-V, RL and BL) or counteract (BL and OL or RL) with light of other wavebands, and their requirements probably depend on the amount of other light. The situations make it difficult to draw a clear formula for lighting. We are required to take a case by case strategy, and gradually to obtain a better combination of individual wavebands. The processes of the development of lighting resembles that of prescription of a culture medium.

For the first step toward lighting formulation, the quantity of PAR should be fixed, because PAR seems to have an absolute quantity requirement. At this step the balance between the RL and BL components in the PAR should be considered. At the next step UV-A should be taken into account. It is less expensive in installment and operation than UV-B, although the functions of UV-A are not clear yet. Finally UV-B comes into consideration. To utilize the

beneficial effects of UV-B and minimizing its deleterious effects, caution should be exercised in the selection of its intensity and waveband.

REFERENCES

Adamse, P. and S. J. Britz. 1992. Amelioration of UV-B damage under high irradiance. I: Role of photosynthesis. Photochem. Photobiol. 56:645-650.

Ahmad, M. and A.R. Cashmore. 1993. HY4 gene of *A. thaliana* encodes a protein with characteristics of a blue-light photoreceptor. Nature 366:162-166.

Aoki, S., Y. Doi and A. Nakayama. 1981. Effect of high irradiance of blue light on the orientation of tea leaves. Japan. Jour. Crop Sci. 50:296-301.

Arakawa, O., Y. Hori, and R. Ogata. 1985. Relative effectiveness and interaction of ultraviolet-B, red and blue light in anthocyanin synthesis of apple fruit. Physiol. Plant. 64:323-327.

Ballare, C. L., P. W. Barnes, and R. E. Kendrick. 1991. Photomorphogenetic effects of UV-B radiation on hypocotyl elongation in wild type and stable-phytochrome-def icient mutant seedlings of cucumber. Physiol. Plant. 83:652-658.

Ballare, C. L., A. L. Scopel, R. A. Sanchez, and S. R. Radosevich. 1992. Photomorphogenetic processes in the agricultural environment. Photochem. Photobiol. 56:777-788.

Baskin, T. I. and M. Iino. An action spectrum in the blue and ultraviolet for phototropism in Alfalfa. Photochem. Photobiol. 46:127-136.

Beggs, C. J. and E. Wellmann. 1985. Analysis of light-controlled anthocyanin formation in coleoptiles of *Zea mays* L.: The role of UV-B, blue, red and far-red light. Photochem. Photobiol. 41:481-486.

Beggs, C. J., E. Wellmann, and H. Grisebach. 1986. Photocontrol of flavonoid biosynthesis. p.467-499. In: R. E. Kendrick and G. H. M. Kronenberg (eds.). Photomorphogenesis in plants. Martinus Nijhoff Publishers, Dordrecht.

Behringer, F. J. and P. J. Davies. 1993. The early time course of the inhibition of stem growth of etiolated pea seedlings by fluorescent light. Plant Growth Regul. 12:341-345.

Bornman, J. F. 1989. New trends in photobiology (invited review) Target sites of UV-B radiation in photosynthesis of higher plants. J. Photochem. Photobiol. B: Biology 4:145-158.

Caldwell, M. M. 1971. Solar UV irradiation and the growth and development of higher plants. p.131-268. In: A. C. Giese (ed.). Photophysiology VI, Academic Press, New York.

Cen, Y. -P. and J. F. Bornman. 1990. The response of bean plants to UV-B radiation under different irradiances of background visible light. J. Exp. Bot. 41:1489-1495.

Cen, Y. -P. and J. F. Bornman. 1993. The effect of exposure to enhanced UV-B radiation on the penetration of monochromatic and polychromatic UV-B radiation in leaves of Brassica napus. Physiol. Plant. 87:249-255.

Chory, J. 1993. Out of darkness: mutants reveal pathways controlling light-regulated development in plants. Trends Genetics 9(5):169-172.

Drumm, H. and H. Mohr. 1978. The mode of interaction between blue (UV) light photoreceptor. Photochem. Photobiol. 27:241-248.

Duell-Pfaff, N. and E. Wellmann. 1982: Involvement of phytochrome and a blue light photoreceptor in UV-B induced flavonoid synthesis in parsley (Petroselinum hortense Hoffm.) cell suspension cultures. Planta 156:213-217..

Ensminger, P. A. 1993. Control of development in plants and fungi by far-UV radiation. Physiol. Plant. 88:501-508.

Flint, S. D., P. W. Jordan, and M. M. Caldwell. 1985. Plant protective response to enhanced UV-B radiation under field conditons: Leaf optical properties and photosynthesis. Photochem. Photobiol. 41:95-99.

Gaba, V. and M. Black. 1979. Two separate photoreceptors control hypocotyl growth in green seedlings. Nature 278:51-54.

Galland, P. and H. Senger. 1988. The role of pterins in the photoreception and metabolism of plants. Photochem. Photobiol. 48:811-820.

Goto, N., K. T. Yamamoto and M. Watanabe. 1993. Action spectra for inhibition of hypocotyl growth of wild-type plants and of the *hy2* long-hypocotyl mutant of *Arabidopsis thaliana* L. Photochem. Photobiol. 57(5):867-871

Hasegawa, S., Y. Tsuboki and H. Fujii. 1979. Effects of coverage with UV-cut-off polyvinyl sheet on the growth of spinach (in Japanese). Nougyou no Kousensentaku Riyougijutsu Kenkyuuhoukokusho 53 nendo:10-21.

Hashimoto, T., N. Kondo, and T. Tezuka. 1993. Harmful and beneficial effects of solar UV light on plant growth. p.551-554. In:A. Shima et al. (eds.). Frontiers of Photobiology. Elsevier Science Publishers B.V. Amsterdam.

Hashimoto, T., C. Shichijo, and H. Yatsuhashi. 1991. Ultraviolet action spectra for the induction and inhibition of anthocyanin synthesis in broom sorghum seedlings. J. Photochem. Photobiol. B: Biol. 11:353-363.

Hashimoto, T., M. Tajima. 1980. Effects of ultraviolet irradiation on growth and pigmentation in seedlings. Plant Cell Physiol. 21:1559-1571.

Iino, M. 1990 Phototropism: mechanisms and ecological implications. Plant Cell Environ. 13:633-650.

Ikenaga, M., S. Kondo, and T. Fujii. 1974. Action spectrum for enzymatic photoreactivation in maize. Photochem. Photobiol. 19:109-113.

Inada, K. 1969. Effect of blue light on the photonastic reaction of rice leaves. Plant Cell Physiol. 10:845-854.

Inada, K. and N. Katsura. 1977. Effect of blue light added to "Youkou Lamp" on the growth of crop plants (in Japanese). Nihon Sakumotsu Gakkai Kiji 46:313-314.

Katsura, N. and K. Inada. 1979. Blue light-induced unrolling in rice plant leaves. Plant Cell Physiol. 20:1071-1077.

Kimura, K. 1974. Effect of light on leaf inclination of *Triticum aestivum* I. Monochromatic light. Ber. Ohara Inst. landw. Biol. 16:47-56.

Kimura, K. 1975. Effect of light on leaf inclination of *Triticum aestivum*. III. Seedling age and photosensitive region. ibid. 16:135-146.

Koller, D. 1990. Light-driven leaf movements. Plant, Cell and Environment 13:615-632.

Liscum, E., J. C. Young, K. L. Poff and R. P. Hangarter. 1992. Genetic separation of phototropism and blue light inhibition of stem elongation. Plant Physiol. 100:267-271.

Maekawa, S., M. Terabun, and M. Nakamura. 1980. Effects of ultraviolet and visible light on flower pigmentation of 'Ehigasa' roses. J. Japan Soc. Hort. Sci. 49:251-259.

Matsunaga, T., K. Hieda and O. Nikaido. 1991. Wavelength dependent formation of thymine dimers and (6-4)photoproducts in DNA by monochromatic ultraviolet light ranging from 150 to 365 nm. Photochem. Photobiol. 54(3):403-410.

Mihara, Y,, H. Sakai, and H. Nishimura. 1973. The effects of UV on plant growth and pigmentation (in Japanese). Proc. 1973 Spring Meeting, Japan. Soc. Hort. Sci., p.202-203.

Nakamura, H., H. Yamada and T. Shimizu. 1977. Studies on the effects of light quality on the growth and development of vegetable crops. II. Effects of light quality obtained

from solar radiation. Yasai Shikenjo Houkoku, A 3:63-80.

Nakayama, A. and Y. Doi. 1977. Effect on the orientation of growing tea leaves of the exclusion of violet-blue band exclusion from solar or artificial white light (in Japanese). Nihon Sakumotsu Gakkai Kiji 46 (Supl.2):125-126.

Ng, Y. L., K. V. Thimann, and S. A. Gordon. 1964. The biogenesis of anthocyanins X. The action spectrum for anthocyanin formation in *Spirodela oligorrhiza*. Arch. Biochem. Phiophys. 107:550-558.

Nouchi, I., K. Kobayashi, and T. Hosono. 1993. Assessment of the effects of enhanced UV-B on agricultural crop plants. Chikyukankyo Kenkyu Sogosuishinhi Nenjihokokusho. Environment Agency of Japan.

Palomares, R., R. G. Hermann and R. Oelmüller. 1991. Different blue-light requirement for the accumulation of transcripts from nuclear genes for thylakoid proteins in Nicotiana tabacum and Lycopersicon esculentum. J. Photochem. Photobiol. B:Biol. 11:151-162.

Parker, K., T.I. Baskin, W.R. Briggs. 1989. Evidence for phytochrome-mediated phototropism in etioloated pea seedlings. Plant Physiol. 89:493-497.

Quiñones, M.A. and E. Zeiger. 1994. A putative role of the zanthophyll, zeaxanthin, in blue light photoreception of corn coleoptiles. Science. 264:558-561.

Rosenstein, B. S. and D. L. Mitchell. 1987. Action spectra for the induction of pyrimidine(6-4)pyrimidone photoproducts and cyclobutane pyrimidine dimers in normal human skin fibroblasts. Photochem. Photobiol. 45:775-780.

Saito, N. and H. Werbin. 1969. Action spectrum for a DNA-photoreactivating enzyme isolated from higher plants. Radiation Botany 9:421-424.

Sasakawa, H. and Y. Yamamoto. 1980. Effects of blue and red light on unrolling of rice leaves. Planta 147:418-421.

Schmelzer, E., W. Jahnen, and K. Hahlbrock. 1988. In situ localization of light-induced chalcone synthase mRNA, chalcone synthase, and flavonoid end products in epidermal cells of parsley leaves. Proc. Natl. Acad. Sci. USA 85:2989-2993.

Shibata, H. 1993. Effects of near ultraviolet light on plant growth (in Japanese). p.12-19. In: Y. Honda (ed.), Heisei 4 nendo Tokuteikenkyuhi Kenkyuseika Houkokusho, Shimane University, Shimane, Japan.

Short, T.W. and W.R. Briggs. 1994. The transduction of blue light signals in higher plants. Annu. Rev. Plant Physiol. Mol. Biol. 45:143-171.

Steinmetz, V. and E. Wellmann. 1986. The role of solar UV-B in growth regulation of cress (Lepidium sativum L.) seedlings. Photochem. Photobiol. 43:189-193.

Takeda, J. and S. Abe. 1992. Light-induced synthesis of anthocyanin in carrot cells in suspension--IV. The action spectrum. Photochem. Photobiol. 56:69-74

Teramura, A. H., R. H. Biggs, and S. Kossuth. 1980. Effects of ultraviolet-B irradiances on soybean. Plant Physiol. 65:483-488.

Tevini, M., J. Braun, and G. Fieser. 1991. The protective function of the epidermal layer of rye seedlings against ultraviolet-B radiation. Photochem. Photobiol. 53:329-333.

Tevini, M. and A. H. Teramura. 1989. UV-B effects on terrestrial plants. Photochem. Photobiol. 50:479-487.

Tezuka, T., T. Hotta, and I. Watanabe. 1993. Growth promotion of tomato and radish plants by solar UV radiation reaching the Earth's surface. J. Photochem. Photobiol. B: Biol., 19:61-66.

Thimann, K. V. and G.M. Curry. 1960. Phototaxis. p.243-306. In: M. Florkin and H. Mason (eds.) Comparative Biochemistry 1. Academic Press, New York.

Wellmann, E., U. Schneider-Ziebert, and C. J. Beggs. 1984. UV-B inhibition of phytochrome-mediated anthocyanin formation in Sinapis alba L. cotyledons. Plant Physiol. 75:997-1000.

Wildermann, A., H. Drumm, E. Schaefer, and H. Mohr. 1978. Control by light of hypocotyl growth in de-etiolated mustard seedlings. 1. Phytochrome as the only photoreceptor pigment. Planta 141:211-216.

Yamada, E., H. Nakamura and T. Shimizu. 1977. Studies on the the effects of light quality on the growth and development of vegetable crops. I Effects of light quality obtained from white light by removing the various spectral regions. Yasai Shikenjo Houkoku, A3:43-61.

Yatsuhashi, H. and T. Hashimoto. 1985. Multiplicative action of a UV-B photoreceptor and phytochrome in anthocyanin synthesis. Photochem. Photobiol. 41(6):673-680.

Yatsuhashi, H., T. Hashimoto, and S. Shimizu. 1982. Ultraviolet action spectrum for anthocyanin formation in broom sorghum internodes. Plant Physiol. 70:735-741.

Zeiger, E. 1983. The biology of stomatal guard cells. Annu. Rev. Plant Physiol. 34:441-475.

ANIMAL & HUMAN REQUIREMENTS