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Photocontrol of Anthocyanin Synthesis

VII. FACTORS AFFECTING THE SPECTRAL SENSITIVITY OF ANTHOCYANIN SYNTHESIS IN YOUNG SEEDLINGS[1]

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ALBERTO L. MANCINELLI AND LYLE WALSH
Department of Biological Sciences, Columbia University in the City of New York, New York 10027

ABSTRACT

Light-dependent anthocyanin synthesis is a typical high irradiance response (HIR) of plant photomorphogenesis. The spectral sensitivity of this response in young seedlings of cabbage and tomato is strongly affected by the length and mode of application of the light treatments. This observation suggests that the different experimental conditions, used in different action spectroscopy studies, might have been responsible, at least in part, for some of the reported differences in the characteristics of the HIR action spectra of different response-system combinations. In both cabbage and tomato, the values of the far red/blue, far red/red, and blue/red action ratios increase with increasing durations of the light treatments; this finding is in agreement with hypotheses of K. M. Hartmann (1966, 1967) and E. Schäfer (1975) for phytochrome action in the HIR. The similarity in the trend of change of the values of the action ratios suggests the possibility that the photomorphogenic pigment system, involved in the photoregulation of anthocyanin synthesis, may be the same in cabbage and tomato, even though there are some differences in the spectral sensitivity of the response between the two species.

The measurement of action spectra is the first step taken toward the identification of the pigment system acting as the photoreceptor for a given photoresponse. The action spectroscopy studies of the HIR (high irradiance responses of plant photomorphogenesis whose full expression requires prolonged exposures to high irradiances of visible and near visible radiation) have shown that there are large differences in the spectral sensitivity of different response-system combinations (Fig. 4 of ref. 16; Figs. 3.8 and 3.9 of ref. 15; Table II of ref. 9). Differences have been found in the wavelengths of the peaks of action and in the combinations and relative efficiencies of the effective spectral regions (1–3, 6, 7, 9, 13–16). As an example, consider the differences in the spectral sensitivity of anthocyanin synthesis in young seedlings: BL[2] is the only effective region in sorghum (2); BL and FR are about equally effective in mustard (17); FR is more effective than BL in turnip (13); and BL is more effective than FR in tomato (11). The causes of these differences are still poorly understood and are partly responsible for the state of uncertainty about the nature of the HIR photoreceptor (9, 15).

There are some points that are seldom mentioned when the data of the action spectroscopy studies are used in discussions about the possible identity of the HIR photoreceptor. (*a*) The experimental conditions (length, irradiance and mode of application of the light treatments, temperature, age of the system) used in different studies vary quite widely, as shown by the short list given in Table I. (*b*) Complete data for the dose response curves and for the time course of the responses under irradiation with different spectral regions are not always available. (*c*) There are some data which show that the spectral sensitivity of some HIR responses can be markedly affected by the irradiance and duration of the exposure and by the age of the system (3, 11, 17). When these points are taken into consideration, it becomes rather difficult to establish the real significance of the differences in the spectral sensitivity of different HIR responses. Are these differences a manifestation of differences in the nature of the HIR photoreceptor of the different response-system combinations? Or are they a manifestation of differences in the operational state of the same photoreceptor and/or in the physiological state of the biological systems, brought about by the different experimental conditions used?

With the hope of being able to achieve some clarification of these problems, we have started a comparative study of the spectral sensitivity of the HIR. In the first stage of our planned research, wide spectrum light sources will be used to determine the action of various factors (length, irradiance and mode of application of the light treatments, age of the system, temperature) on the spectral sensitivity of the HIR of different response-system combinations. The data obtained in the first stage will provide a basic reference standard for a comparative analysis of the spectral sensitivity of the HIR and the information necessary to carry out detailed action spectroscopy studies later on. Here we report some results obtained in a study of the effects of duration and mode of application of the light treatments on the spectral sensitivity of anthocyanin synthesis in cabbage and tomato seedlings.

MATERIALS AND METHODS

Seeds of cabbage (*Brassica oleracea*, Red Acre) and tomato (*Lycopersicon esculentum*, Beefsteak) were germinated and grown in darkness at 20 C, in Petri dishes, on filter paper moistened with H_2O. The light treatments were started 72 h after sowing for cabbage and 96 h after sowing for tomato. The light treatments were given in growth chambers equipped with wide spectrum light sources (8). The irradiances of the BL, R, and FR sources were adjusted to provide a quantum flux density of 1,700 ± 100 pE s^{-1} cm^{-2}. The quantum flux densities of the W light source were about 1,050, 2,600 and 1,700 pE s^{-1} cm^{-2} in the BL, R, and FR regions, respectively. The integral dark red filter of the BCJ lamps transmits radiation at wavelengths longer than 650 nm (8); the quantum flux density of the BCJ source was about 1,600 pE s^{-1} cm^{-2} in the FR region, and about 650 pE s^{-1} cm^{-2} in the 650–700 nm region. The values of the Pfr/P ratio at photoequilibrium, determined in cabbage seedlings and in a partially purified phytochrome solution

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[2] Abbreviations: BCJ: incandescent lamps with an integral dark red filter, having a cut-off at about 650 nm; BL: blue; R: red; FR: far red; W: white; HIR: high irradiance response; P: total phytochrome = Pr + Pfr; TD: total duration of exposure.

Table I. A short list to illustrate some of the differences in the experimental conditions used in different action spectroscopy studies of the HIR

ANTHOCYANIN SYNTHESIS		
1. Red cabbage	(13)*	4 h MCI - 5 min R - 24 h D; WR: 400-900 nm
2. Turnip	(13)*	2 h WF - 8 h MCI - 5 min R - 24 h D; WR: 400-900 nm
3. Sorghum	(2)*	4 h WF - 36 x (5 min MCI - 5 min D) - 5 min R - 14 h D; WR: 390-680 nm
4. Turnip	(4)*	48 h MCI; WR: 625-780 nm
5. Apple skin	(14)*	
a. Induction period		12 h MCI - 20 or 28 h WF - 24 h D; WR: 550-750 nm
b. Linear period		32 or 40 h WF - 12 h MCI; WR: 400-800 nm
INHIBITION OF HYPOCOTYL ELONGATION		
6. Lettuce	(3)*	8 h MCI - 5 min R - 16 h D; WR: 400-800 nm
7. Lettuce	(6)*	18 h MCI; WR: 320-1000 nm
8. Petunia	(3)*	3 or 4 x (4 h MCI - 5 min R - 20 hr D); WR: 400-800 nm
9. Radish	(7)*	24 h MCI; WR: 400-800 nm

* Literature reference. MCI: monochromatic irradiations. WF: white fluorescent light. WR: wavelength range. R: red. D: dark.

from squash seedlings, were the following: 0.30 to 0.35 for the BL; 0.75 for the R; less than 0.05 for the FR; 0.65 to 0.70 for the W; and 0.20 to 0.25 for the BCJ source.

The pigments were extracted in all cases 72 h after the beginning of the light treatments. Lots of 30 cabbage seedlings or 60 tomato seedlings each were extracted with acidified methanol (1% HCl, w/v) for 2 days, at 2 to 5 C, with continuous shaking. The extracts were clarified by filtration and their A at 530 and 657 nm were measured with a Gilford 300-N spectrophotometer. For anthocyanin, the A values of the extracts (Tables II and III) are given as $A_{530} - 0.33A_{657}$ (10). The A values used for Chl are those of the acidic methanol extracts at 657 nm; there is a linear relationship between the A_{657} value of the acidic methanol extracts and the total Chl content of the seedlings (18). The values reported in Tables II and III are the average of a minimum of eight replicates in two independent experiments.

The effectivenesses (Tables II and III) of the light treatments for pigment production are the values of the ratio:

$$\frac{\text{Absorbance of the extract}}{\text{Total incident energy}}$$

The total incident energy is given in mE cm^{-2}. The action ratios (Tables IV and V) are the values of the ratio between the effectivenesses of two light sources; *e.g.* the FR/BL action ratio is the value of the ratio:

$$\frac{\text{Effectiveness of FR}}{\text{Effectiveness of BL}}$$

RESULTS

Light-dependent pigment production (Tables II and III) is a function of the duration and mode of application of the light treatments and is higher in cabbage than in tomato.

Insofar as the effectiveness of the various light treatments for pigment production is concerned (Tables II and III), we can distinguish the following groups. (*a*) Anthocyanin synthesis in cabbage: the effectiveness decreases with increasing duration of the exposure under both the continuous (treatments 01–06) and the photoperiodic (treatments 09–13) light treatments; (*b*) Anthocyanin synthesis in tomato: the effectiveness first increases and then decreases with increasing durations of the exposures; (*c*) Chl synthesis: the effectiveness increases with increasing durations of the continuous exposures in both species; the effectiveness first increases (tomato), or remains about the same (cabbage), and then decreases with increasing lengths of the photoperiod. The photoperiodic light treatments are less effective for anthocyanin synthesis and more effective for Chl synthesis than the continuous ones, as shown, for example, by a comparison of the effects of treatments numbers 04 and 11 (total length of the exposure = 24 h); these differences in effectiveness are larger in tomato than in cabbage. (*d*) The short cycled light treatments (treatments 14–16) have very high effectivenesses, generally higher than those of continuous or photoperiodic light treatments with the same or very close total durations of the exposures; *e.g.* compare the effects of treatments 02, 09, and 14 with a total duration of the exposures between 6 and 9 h, and of treatments 10, 15, and 16 with a total duration of the exposure of 18 h.

The duration and mode of application (continuous, photoperiodic, short cycled) of the light treatments have a marked effect on the spectral sensitivity of anthocyanin production, as shown by the large changes in the values of the action ratios (Tables IV and V). The relative effectiveness of FR for anthocyanin production increases with increasing durations of the exposures and with a shortening of the cycles, as shown by the increase in the values of the FR/BL, FR/R, FR/BCJ, and FR/W action ratios. The values of these action ratios are larger in cabbage than in tomato, but the general trend of change of the values is similar in the two species. A similarity of behavior between the two species can also be seen in the trend of change of the values of the other action ratios, BL/R, BL/BCJ, BL/W, and BCJ/W. Although a complete study of the action of temperature has not been carried out, it seems evident (treatments 06–08) that this factor can have a pronounced effect on both the effectiveness and the spectral sensitivity of anthocyanin synthesis.

The effects of the duration and mode of application of the light treatments on the spectral sensitivity of Chl production are not as pronounced as those found for anthocyanin production.

DISCUSSION

In cabbage and tomato seedlings, the spectral sensitivity of light-dependent anthocyanin production, a typical HIR response, is not constant and is markedly affected by the duration and mode of application (continuous, photoperiodic, short cycled) of the light treatments and by the temperature. The range of durations

Table II. Action of various light treatments on the synthesis of anthocyanin and chlorophyll in cabbage seedlings

The pigments were extracted 72 hours after the beginning of the light treatments. The temperature during the light treatments was 20 C, except as noted. For each treatment, the numbers on the first line are the absorbance values of the extracts ($A_{530} - 0.33A_{657}$ for anthocyanin; A_{657} for chlorophyll), corrected by subtracting the absorbance values of the dark controls; the underlined numbers on the second line are the effectiveness values. The average absorbance values of the dark control extracts were 0.24 for anthocyanin and 0.02 for chlorophyll. L: light; D: darkness; TD: total length of the exposure to light.

	ANTHOCYANIN					CHLOROPHYLL				
LIGHT TREATMENTS	BL	R	FR	BCJ	W	BL	R	FR	BCJ	W
01. 3 h L - 69 h D	0.24	0.29	0.14	0.27	0.36	0.007	0.009	0.001	0.008	0.006
TD: 3 h	13.07	15.79	7.63	11.11	6.23	0.38	0.49	0.05	0.33	0.16
02. 6 h L - 66 h D	0.36	0.42	0.28	0.45	0.48	0.026	0.027	0.006	0.029	0.032
TD: 6 h	9.80	11.44	7.63	9.26	4.15	0.71	0.74	0.16	0.60	0.28
03. 12 h L - 60 h D	0.62	0.48	0.50	0.71	0.69	0.069	0.065	0.009	0.066	0.004
TD: 12 h	8.44	6.54	6.81	7.31	2.99	0.94	0.89	0.12	0.68	0.41
04. 24 h L - 48 h D	0.73	0.55	0.95	1.04	0.91	0.13	0.18	0.011	0.083	0.16
TD: 24 h	4.97	3.75	6.47	5.35	1.97	0.89	1.23	0.08	0.43	0.35
05. 48 h L - 24 h D	0.92	0.64	1.26	1.44	1.11	0.42	0.48	0.033	0.27	0.55
TD: 48 h	3.13	2.18	4.29	3.70	1.20	1.43	1.63	0.11	0.69	0.60
06. 72 h L	1.14	0.65	1.58	1.44	1.33	0.60	0.63	0.041	0.42	0.76
TD: 72 h	2.59	1.48	3.59	2.47	0.96	1.36	1.43	0.09	0.72	0.55
07. 72 h L at 25 C	0.87	0.65	1.22	1.20	0.91	0.57	0.63	0.044	0.41	0.69
TD: 72 h	1.97	1.48	2.77	2.06	0.66	1.29	1.43	0.10	0.70	0.50
08. 72 h L at 15 C	0.83	0.58	1.25	1.31	1.28	0.38	0.42	0.031	0.31	0.50
TD: 72 h	1.88	1.32	2.84	2.25	0.92	0.86	0.95	0.07	0.53	0.43
09. 3 x (3 h L - 21 h D)	0.52	0.46	0.23	0.65	0.68	0.10	0.12	0.007	0.092	0.17
TD: 9 h	9.44	8.35	4.18	8.92	3.92	1.82	2.18	0.13	1.26	0.98
10. 3 x (6 h L - 18 h D)	0.59	0.55	0.54	0.90	0.79	0.20	0.24	0.013	0.20	0.37
TD: 18 h	5.36	4.99	4.90	6.17	2.28	1.82	2.18	0.12	1.37	1.07
11. 3 x (8 h L - 16 h D)	0.68	0.50	0.58	0.98	0.83	0.29	0.27	0.021	0.23	0.41
TD: 24 h	4.63	3.40	3.95	5.04	1.80	1.97	1.84	0.14	1.18	0.89
12. 3 x (12 h L - 12 h D)	0.84	0.53	0.92	1.16	1.00	0.41	0.43	0.026	0.28	0.58
TD: 36 h	3.81	2.41	4.18	3.98	1.44	1.86	1.95	0.12	0.96	0.84
13. 3 x (18 h L - 6 h D)	0.90	0.68	1.16	1.34	1.18	0.49	0.53	0.038	0.37	0.69
TD: 54 h	2.72	2.06	3.51	3.06	1.14	1.48	1.60	0.12	0.85	0.66
14. 4320 x (6 s L - 54 s D)	0.56	0.50	0.99	0.78	0.70	0.26	0.41	0.024	0.18	0.46
TD: 7.2 h	12.71	11.35	22.47	13.37	5.05	5.90	9.31	0.55	3.09	3.32
15. 360 x (3 min L - 9 min D)	0.73	0.49	0.88	0.79	0.78	0.41	0.46	0.021	0.25	0.51
TD: 18 h	6.63	4.45	7.99	5.42	2.25	3.72	4.18	0.19	1.72	1.47
16. 12 x (90 min L - 270 min D)	0.83	0.56	0.46	0.68	0.96	0.26	0.31	0.013	0.21	0.42
TD: 18 h	7.53	5.08	4.18	4.66	2.77	2.36	2.81	0.12	1.44	1.21

Effectiveness value = (Absorbance of the extract)/(Total incident energy)

and modes of application of the light treatments, used in our study, covers quite well the range of the differences in the experimental conditions that have been used in different action spectroscopy studies of the HIR (Table I). Differences in the duration and mode of application of the light treatments result in rather large differences in the spectral sensitivity of anthocyanin production in our test systems. In cabbage (Tables II and IV), the most effective spectral region can be R or BL or FR, depending upon the conditions used; in particular, observe the high effectiveness of FR under the short cycled light treatment 14, with a TD of 7.2 h. In tomato (Tables III and V), the most effective spectral region can be either R or BL; FR is generally much less effective than R and BL, but, under the short cycled treatment 14, it can be almost as effective as R and BL.

Our results were obtained using exposures to wide spectrum light sources and cannot provide the fine details of the spectral characteristics of a photoresponse that can be obtained with the use of monochromatic light sources. Despite this limitation, our data suggest that the differences in the experimental conditions, used in the various studies (Table I), might have been responsible, at least in part, for the differences that have been observed in the HIR action spectra of different response-system combinations (1–3, 6, 7, 13–16). The fact that the spectral sensitivity of a given HIR response can change, depending upon the experimental conditions used, should not be considered only as a complicating factor in the identification of the HIR photoreceptor. Data on the trends of change of the spectral sensitivity can be useful for a comparative analysis of the spectral characteristics of different HIR responses and for the study of the relationships between the changes in the photosensitivity of the response and the changes in the state of the pigments that are being considered as candidates for the role of photoreceptor. The study of these relationships is an important step for both the identification of the photoreceptor and the elucidation of its mechanism of action.

The differences in the spectral sensitivity of anthocyanin synthesis in cabbage and tomato are rather large, as shown by the differences in the relative effectiveness of FR (Tables II to V). This observation could be considered as indicative of a difference in the nature of the photoreceptor in the two species, but this interpretation is not entirely supported by other observations. (*a*) The photoreceptor systems of both species have absorption in the BL, R, and FR regions of the spectrum (Tables II and III). (*b*)

Table III. Action of various light treatments on the synthesis of anthocyanin and chlorophyll in tomato seedlings

Details as in Table II. The average absorbance values of the dark control extracts were 0.01 for anthocyanin and 0.02 for chlorophyll.

LIGHT TREATMENTS	ANTHOCYANIN					CHLOROPHYLL				
	BL	R	FR	BCJ	W	BL	R	FR	BCJ	W
01. 3 hr L - 69 h D	0.006	0.019	0.000	0.010	0.026	0.003	0.006	0.001	0.005	0.004
TD: 3 h	0.33	1.04	0.00	0.41	0.45	0.16	0.33	0.05	0.21	0.07
02. 6 hr L - 66 h D	0.046	0.050	0.002	0.043	0.092	0.010	0.009	0.004	0.011	0.009
TD: 6 h	1.25	1.36	0.05	0.89	0.80	0.27	0.25	0.11	0.23	0.08
03. 12 hr L - 60 h D	0.11	0.13	0.015	0.14	0.21	0.022	0.021	0.007	0.022	0.020
TD: 12 h	1.50	1.77	0.20	1.44	0.91	0.30	0.29	0.09	0.23	0.09
04. 24 hr L - 48 h D	0.17	0.14	0.040	0.17	0.26	0.047	0.035	0.008	0.040	0.057
TD: 24 h	1.16	0.95	0.27	0.87	0.56	0.32	0.24	0.05	0.21	0.12
05. 48 hr L - 24 h D	0.23	0.17	0.053	0.21	0.34	0.16	0.18	0.022	0.17	0.21
TD: 48 h	0.78	0.58	0.18	0.54	0.37	0.55	0.61	0.08	0.44	0.23
06. 72 hr L	0.22	0.17	0.077	0.26	0.32	0.37	0.33	0.033	0.29	0.32
TD: 72 h	0.50	0.39	0.18	0.45	0.23	0.84	0.75	0.08	0.50	0.23
07. 72 hr L at 25 C	0.17	0.10	0.028	0.12	0.24	0.53	0.37	0.040	0.32	0.46
TD: 72 h	0.39	0.23	0.06	0.21	0.17	1.20	0.84	0.09	0.55	0.33
08. 72 hr L at 15 C	0.28	0.16	0.058	0.20	0.40	0.21	0.14	0.019	0.18	0.23
TD: 72 h	0.64	0.36	0.13	0.34	0.29	0.48	0.32	0.04	0.31	0.17
09. 3 x (3 h L - 21 h D)	0.030	0.033	0.005	0.033	0.076	0.046	0.054	0.008	0.051	0.061
TD: 9 hr	0.55	0.60	0.09	0.45	0.44	0.84	0.98	0.15	0.70	0.35
10. 3 x (6 hr L - 18 h D)	0.069	0.064	0.009	0.084	0.17	0.13	0.12	0.013	0.11	0.18
TD: 18 hr	0.63	0.58	0.08	0.58	0.49	1.18	1.09	0.12	0.75	0.52
11. 3 x (8 h L - 16 h D)	0.11	0.087	0.020	0.11	0.21	0.23	0.22	0.016	0.17	0.34
TD: 24 h	0.75	0.59	0.14	0.57	0.45	1.57	1.50	0.11	0.87	0.74
12. 3 x (12 h L - 12 h D)	0.14	0.11	0.042	0.17	0.26	0.33	0.27	0.026	0.20	0.35
TD: 36 hr	0.64	0.50	0.19	0.58	0.38	1.50	1.23	0.12	0.69	0.51
13. 3 x (18 hr L - 6 h D)	0.18	0.15	0.061	0.19	0.30	0.36	0.30	0.037	0.24	0.35
TD: 54 hr	0.55	0.45	0.19	0.43	0.29	1.09	0.91	0.11	0.55	0.34
14. 4320 x (6 s L - 54 s D)	0.12	0.11	0.11	0.15	0.18	0.32	0.34	0.028	0.17	0.33
TD: 7.2 h	2.72	2.50	2.50	2.57	1.30	7.26	7.72	0.64	2.92	2.38
15. 360 x (3 min L - 9 min D)	0.15	0.12	0.10	0.16	0.21	0.34	0.33	0.027	0.21	0.28
TD: 18 h	1.36	1.09	0.91	1.10	0.61	3.09	3.00	0.25	1.44	0.81
16. 12 x (90 min L - 270 min D)	0.15	0.12	0.023	0.12	0.25	0.17	0.18	0.020	0.16	0.18
TD: 18 h	1.36	1.09	0.21	0.82	0.72	1.54	1.63	0.18	1.10	0.52

The general trend of changes in the values of the action ratios (Tables IV and V), especially FR/BL, FR/R, FR/BCJ, and FR/W, is very similar in the two species. These two observations are consistent with the possibility that the HIR photoreceptor system for anthocyanin synthesis might be the same in the two species and that some other factors might be responsible for the differences in the spectral sensitivity of the response between cabbage and tomato. With the data available at present it is not possible to define the nature of these other factors. Just as a working hypothesis, one might consider the possibility of differences in one or more of the following factors: (*a*) degree of interaction between two photoreceptors; (*b*) amount of self- and/or foreign pigment screening; (*c*) operational state of the photoreceptor; (*d*) the rate of the reaction between the active form of the photoreceptor and its reaction partner; (*e*) degree of photomorphogenic competence for anthocyanin synthesis and physiological state of the system; (*f*) value of the photoequilibrium ratio:

$$\frac{\text{Active form of the photoreceptor}}{\text{Total amount of the photoreceptor}}$$

required for maximum action.

The increase in the values of the FR/BL, FR/R, and BL/R action ratios with increasing duration of the exposures can be predicted on the basis of the hypotheses of Hartmann (5) and Schäfer (12) for phytochrome action in the HIR. Insofar as anthocyanin synthesis in cabbage seedlings is concerned, the increase in the values of the FR/BL, FR/R, and BL/R action ratios with increasing duration of the exposures (Table IV) shows a good correlation with the time course of the changes of the levels of phytochrome and Pfr in seedlings exposed to continuous BL, R, and FR (11).

Action spectroscopy studies are only the first step toward the identification of the photoreceptor of any given photoresponse or class of photoresponses; the development of the successive steps depends upon the results of such studies and may become rather difficult if there is a scarcity of data for the evaluation of the significance of the differences between different action spectra, such as in the case of different HIR responses. The definition of the general characteristics of the HIR requires, among other things, a comparative analysis of the spectral characteristics of the HIR of different response-system combinations; a meaningful comparative analysis cannot be made without full data on the action of several factors, *e.g.* duration, irradiance and mode of application of the light treatments, upon the spectral characteristics of the responses. Any working hypothesis about the identity of the HIR photoreceptor, based on the available data from action spectroscopy studies, should give full consideration to the effects that the differences in experimental conditions (Table I) might have had on the outcome of such studies.

Table IV. The effects of duration and mode of application of the light treatments on the relative effectiveness of different light sources for anthocyanin synthesis in cabbage seedlings

The values of the action ratios were calculated from the effectiveness values for anthocyanin synthesis of Table II. See the last paragraph of the "Materials and Methods" section for a definition of action ratio.

Light Treatments*	Values of indicated action ratios							
	FR/BL	FR/R	FR/BCJ	FR/W	BL/R	BL/BCJ	BL/W	BCJ/W
01	0.58	0.48	0.69	1.22	0.83	1.18	2.10	1.78
02	0.78	0.67	0.82	1.83	0.86	1.06	2.36	2.23
03	0.81	1.04	0.93	2.28	1.29	1.16	2.83	2.45
04	1.30	1.73	1.21	3.28	1.33	0.93	2.52	2.72
05	1.37	1.97	1.16	3.57	1.44	0.85	2.61	3.08
06	1.39	2.43	1.45	3.74	1.75	1.05	2.70	2.57
07	1.40	1.88	1.35	4.22	1.34	0.96	3.01	3.14
08	1.51	2.16	1.26	3.07	1.43	0.84	2.04	2.43
09	0.44	0.50	0.47	1.06	1.13	1.06	2.41	2.27
10	0.92	0.98	0.79	2.15	1.07	0.87	2.35	2.71
11	0.85	1.16	0.78	2.20	1.36	0.92	2.58	2.81
12	1.10	1.74	1.05	2.90	1.58	0.96	2.64	2.76
13	1.29	1.71	1.15	3.09	1.32	0.89	2.40	2.70
14	1.77	1.98	1.68	4.45	1.12	0.95	2.52	2.65
15	1.21	1.80	1.47	3.55	1.49	1.22	2.94	2.41
16	0.55	0.82	0.90	1.51	1.48	1.62	2.72	1.68

* Light treatments indicated by number only; see Table II for details.

Table V. The effects of duration and mode of application of the light treatments on the relative effectiveness of different light sources for anthocyanin synthesis in tomato seedlings

The values of the action ratios were calculated from the effectiveness values for anthocyanin synthesis of Table III. See the last paragraph of the "Materials and Methods" section for the definition of action ratio.

Light Treatments*	Values of indicated action ratios							
	FR/BL	FR/R	FR/BCJ	FR/W	BL/R	BL/BCJ	BL/W	BCJ/W
01	0.00	0.00	0.00	0.00	0.32	0.80	0.73	0.91
02	0.04	0.04	0.06	0.07	0.92	1.42	1.57	1.11
03	0.14	0.12	0.14	0.22	0.85	1.04	1.67	1.68
04	0.24	0.29	0.31	0.48	1.21	1.32	2.06	1.56
05	0.23	0.31	0.33	0.49	1.35	1.45	2.13	1.47
06	0.35	0.45	0.39	0.76	1.29	1.12	2.16	1.93
07	0.17	0.28	0.31	0.37	1.70	1.87	2.23	1.19
08	0.21	0.36	0.38	0.46	1.75	1.85	2.20	1.19
09	0.17	0.16	0.20	0.21	0.91	1.20	1.24	1.03
10	0.13	0.14	0.14	0.17	1.08	1.09	1.28	1.18
11	0.18	0.23	0.24	0.30	1.27	1.32	1.65	1.25
12	0.30	0.38	0.33	0.51	1.27	1.09	1.69	1.55
13	0.34	0.41	0.43	0.64	1.20	1.26	1.89	1.51
14	0.92	1.00	0.97	1.92	1.09	1.06	2.10	1.98
15	0.67	0.83	0.83	1.50	1.25	1.24	2.24	1.81
16	0.15	0.19	0.25	0.29	1.25	1.65	1.89	1.14

* Light treatments indicated by number only; see Table III for details.

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