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Photocontrol of Anthocyanin Synthesis

IV. DOSE DEPENDENCE AND RECIPROCITY RELATIONSHIPS IN ANTHOCYANIN SYNTHESIS[1]

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ABSTRACT

Under continuous far red light, anthocyanin synthesis in young, dark-grown cabbage seedlings (*Brassica oleracea* cv. Red Acre) is irradiance-dependent and fails to follow the reciprocity (irradiance × time = constant) relationships. Under intermittent far red treatments extended over a prolonged period of time, anthocyanin synthesis becomes dose dependent, and reciprocity relationships are valid. Intermittent far red treatments with short dark intervals between successive irradiations are as effective as continuous treatments, if the total radiation doses applied with the two types of treatments are equal and are applied over equally long periods of time. The high effectiveness of intermittent treatments, the dose dependence, and the validity of the reciprocity relationships suggest that cycling between red-absorbing form of phytochrome and far red-absorbing form of phytochrome and the formation of electronically excited far red-absorbing form of phytochrome, or the involvement of a second photoreactive system, besides phytochrome, may play only a minor role in high irradiance reaction anthocyanin synthesis brought about by prolonged exposures to far red irradiation.

The irradiance dependence and the reciprocity failure of the high irradiance responses of plant photomorphogenesis are responsible for some uncertainty in the interpretation of results obtained in HIR[3] research and for the different hypotheses about the nature of the HIR photoreceptor(s) (2, 4, 6, 7, 14, 19–22).

Limiting the discussion to the HIR photoresponses brought about by continuous FR ($\lambda > 700$ nm) in young seedlings, there are essentially two hypotheses: (*a*) P is the only photoreceptor involved (2, 7, 14); and (*b*) HIR responses arise through an interaction between P and photosynthesis, specifically PSI (19, 20). Action spectra of photoresponses that do not follow the reciprocity law ($I \times t = nI \times t/n = K$) may not resemble the absorption spectrum of the photoreceptor, but some complex function of the interaction between two photoreceptors, and are therefore of little help in clarifying the nature of the HIR photoreceptors.

The evidence (19, 20) in support of the second of the two hypotheses above is not very convincing, and recent results (10, 11) have provided some evidence against the involvement of photosynthesis in the HIR of young seedlings.

According to the first of the two hypotheses, HIR responses are brought about by the low, but relatively constant level of Pfr maintained under continuous FR (2, 7, 14, 22). Maximum HIR effects are obtained at wavelengths near 720 nm where the Pfr/P photoequilibrium ratio is approximately 0.03 (7, 14, 22). The Pfr/P photoequilibrium ratio is a function of wavelength and not of the irradiance (3, 22): therefore HIR responses should be irradiance independent. The irradiance dependence of the HIR has been interpreted as a consequence of the irradiance dependence of the rate of cycling between Pr and Pfr (7), and the formation of Pfr* (14, 21), an excited form of Pfr, physiologically more effective than Pfr (ground state). The equilibrium concentration of Pfr* is a function of the rate of photochemical turnover of Pfr, and therefore of the irradiance (14); the interpretation of Pfr* in physical terms is still an open question (14, 22). It has also been suggested that the irradiance dependence of the HIR may be a consequence of the balance between the rates of the Pr ↔ Pfr photoconversion, of the formation of a physiologically active PfrX complex, and of the photodissociation properties of PfrX (2).

This note deals specifically with one of the aspects of the HIR, namely the reciprocity failure. The fact that, when irradiations are long, the $\{(I \times t)\text{FR}\}$ and $\{(nI \times t/n)\text{FR} + (t - t/n)\text{hr } D\}$ treatments give different quantitative results, is probably a consequence of the characteristics of both the HIR and Pfr. The HIR responses require that a certain level of Pfr be maintained over a long period of time. During the dark period following the light treatment, Pfr disappears in a few hours through dark reversion and irreversible decay (8, 14, 22). Therefore, the two treatments above are not equivalent in terms of the level of Pfr maintained over an extended period of time.

Intermittent light treatments are quite effective in bringing about HIR anthocyanin synthesis (5, 9, 11); intermittent FR treatments with short dark intervals between successive irradiations result in the production of a level of anthocyanins equal to that produced under continuous irradiation, if the total radiation doses applied with the two treatments are equal and are applied over equally long periods (9). Intermittent light treatments with short dark intervals between successive irradiations should maintain a level of Pfr very close to that maintained under continuous irradiation, inasmuch as the dark reversion of Pfr to Pr would be quite small during the short dark intervals, and the rate of irreversible decay would probably be similar to that under continuous irradiation. Under intermittent FR treatments, the presence of Pfr would be limited only to the short light periods during each cycle, and Pfr (ground state) should be the dominant

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[3] Abbreviations: HIR: high irradiance reaction; D: dark; FR: far red; R: red; I: irradiance; P: phytochrome; P′: nonphotoreversible P; Pfr*: electronically excited state of Pfr; PSI: pigment system I of photosynthesis; *t*: time X, X′, X″: receptor sites for P binding in various configurations.

Table I. *Irradiance Dependence of Anthocyanin Synthesis in Cabbage Seedlings Exposed to Continuous FR*

The absorbance values were corrected by subtracting the absorbance values of the dark controls. Numbers in parentheses are total radiations doses (joules cm^{-2}). A: extraction at the end of the FR irradiation; B: extraction 48 hr after the beginning of the FR irradiation; C: extraction as in B; 5 min of R applied at the end of the FR irradiation.

Length of FR Treatment	Absorbance											
	13 $\mu w\ cm^{-2}$			40 $\mu w\ cm^{-2}$			130 $\mu w\ cm^{-2}$			400 $\mu w\ cm^{-2}$		
	A	B	C	A	B	C	A	B	C	A	B	C
hr												
6		0.18	0.39		0.20	0.41		0.25	0.47		0.34	0.50
	(0.28)			(0.86)			(2.8)			(8.6)		
12	0.17	0.37	0.64	0.18	0.52		0.17	0.48	0.73	0.22	0.59	0.84
	(0.56)			(1.7)			(5.6)			(17)		
24	0.38	0.52	0.78	0.56	0.69	0.79	0.61	0.84	1.05	0.76	1.22	
	(1.1)			(3.5)			(11.5)			(35)		
36	0.57	0.70	0.79	0.85	1.05		0.89	1.14	1.20	1.20	1.34	1.48
	(1.7)			(5.2)			(17)			(52)		
48	0.85			0.98			1.31			1.43		
	(2.3)			(6.9)			(23)			(69)		

form of Pfr. Irradiance and duration of the short, repeated light treatments can be easily changed; thus, cyclic light treatments offer the possibility of studying the reciprocity relationships of HIR responses under conditions of prolonged irradiations.

MATERIALS AND METHODS

Seeds of cabbage (*Brassica oleracea*, cv. Red Acre) and mustard (*Sinapis alba*, cv. Fine White) were germinated and grown in darkness at 20 C in Petri dishes (30 seeds/dish) on two disks of Whatman No. 3 filter paper, moistened with distilled H_2O. Light treatments were started 96 (cabbage) or 48 (mustard) hr after planting. The light treatments were given in growth chambers equipped with FR radiation sources that have been described previously (9–11).

Anthocyanin Extraction and Measurements. Lots of 30 seedlings each were extracted with 15 ml of 1% HCl in methanol (w/v) for 2 days at 3 to 5 C, with continuous shaking. The extracts were clarified by filtration, and their absorbances at 530 and 657 nm were measured with a Gilford 300-N spectrophotometer. The formula ($A_{530} - 0.33\ A_{657}$) was used to eliminate the contribution of Chl and its degradation products in acid solution to the absorbance value at 530 nm (10). The results reported are the average of at least eight replicates. Under the experimental conditions used, the average absorbance of the dark controls was about 0.270 to 0.290 for cabbage and 0.035 to 0.045 for mustard.

RESULTS

The dependence on irradiance and duration and the reciprocity failure of anthocyanin synthesis under continuous FR irradiation are clearly shown by the results of Table I. Anthocyanin accumulation, induced by a relatively short (4 hr) FR irradiation, is almost irradiance independent (Fig. 1); the small differences induced by different irradiances disappear completely when the 4-hr FR irradiations are followed by a short exposure to R (Fig. 1C). A short R applied at the end of the FR irradiation enhances anthocyanin accumulation (Table 1, B and C; Fig. 1, A and C).

The mode of application of a given total radiation dose is very important in determining the extent of anthocyanin accumulation. For example, a dose of 2.8 joules cm^{-2}, applied as a 6-hr irradiation at 130 $\mu w\ cm^{-2}$ (Table I), is much less effective than slightly lower or about equal doses applied either continuously (Table I, 2.3 joules, 48 hr at 13 $\mu w\ cm^{-2}$) or as cyclic irradiation treatments (Fig. 3, 3 joules) over a 48-hr period. Equal total radiation doses applied either as continuous irradiation or as intermittent irradiation over the same period of time, yield equal levels of anthocyanin accumulation, if the length of the cycles in the intermittent treatments is kept short (Fig. 2; also compare data of Table I and Fig. 3 for equal radiation doses).

Within the limits established by the characteristics of the radiation sources and of the timers available in our laboratory, cyclic irradiation treatments follow the reciprocity law (Figs. 3 and 4). The differences among the treatments resulting in the application of equal radiation doses are not statistically significant. The data of Figures 3 and 4 also show that under cyclic irradiation anthocyanin accumulation is dose dependent and not irradiance dependent, as it is under continuous irradiation.

The effectiveness of cyclic treatments decreases with increasing

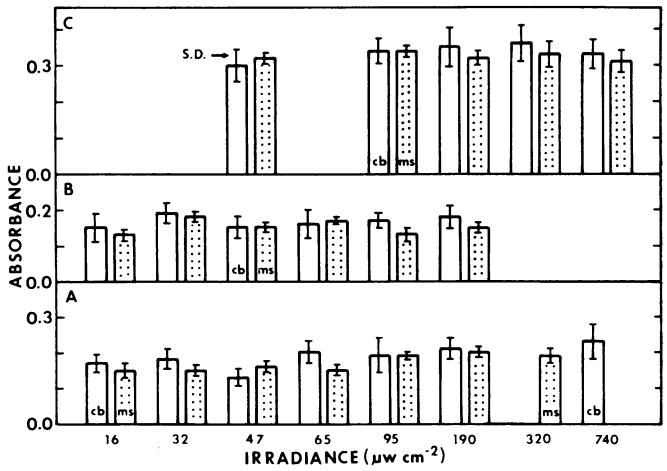

FIG. 1. Action of continuous FR irradiation on the synthesis of anthocyanins in cabbage and mustard seedlings. Anthocyanins were extracted 48 hr after the beginning of the light treatments. The absorbance values reported in the figure were corrected by subtracting the absorbance values of the dark controls. A: 4 hr FR at indicated irradiances; B: 5 min FR at 740 $\mu w\ cm^{-2}$ — 4 hr FR at indicated irradiances; C: 4 hr FR at indicated irradiances — 5 min R; cb: cabbage; ms: mustard; S.D.: standard deviation.

length of the cycle (Table II); this decrease of effectiveness may possibly be a consequence of the decrease of the Pfr level during the dark period of the cycle; as the cycles become longer, the average Pfr level decreases as it is integrated over the total duration of the light treatment. Increasing the length of the cycle

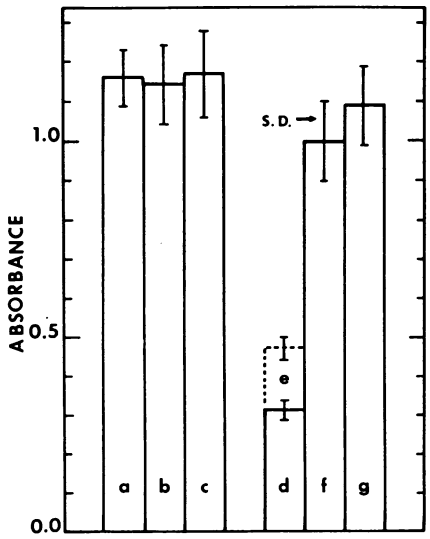

FIG. 2. Action of continuous and intermittent FR irradiations on the synthesis of anthocyanins in cabbage seedlings. Anthocyanins were extracted 48 hr after the beginning of the light treatments. Absorbance values reported in the figure were corrected by subtracting the values of the dark controls. a: 48 hr continuous FR at 100 μw cm^{-2}; b: 48 hr cyclic FR (10 sec ON/10 sec OFF) at 200 μw cm^{-2}; c: 48 hr cyclic FR (5 sec ON/15 sec OFF) at 400 μw cm^{-2}; d: 6 hr continuous FR at 440 μw cm^{-2}; e: 6 hr continuous FR at 440 μw cm^{-2} — 5 min R; f: 48 hr continuous FR at 55 μw cm^{-2}; g: 48 hr cyclic FR (3 sec ON/27 sec OFF) at 550 μw cm^{-2}. Total radiation dose for treatments a, b, and c was 17.3 joules cm^{-2}. Total FR radiation dose for treatments d, e, f, and g was 9.5 joules cm^{-2}. S.D.: standard deviation.

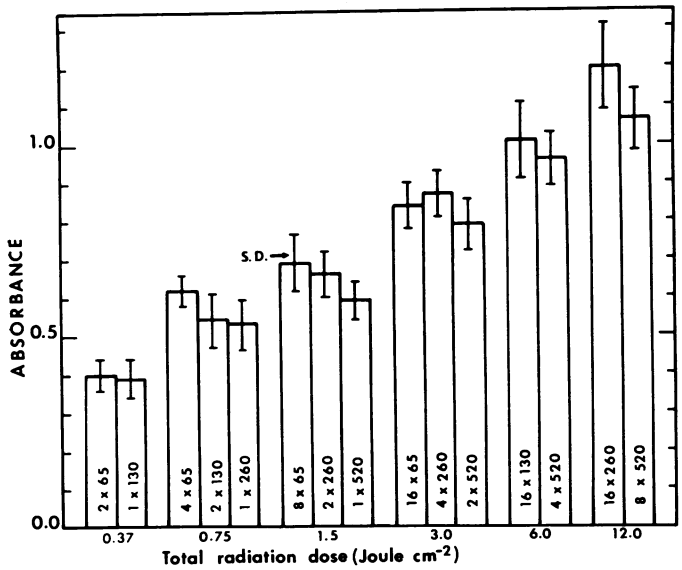

FIG. 3. Action of cyclic FR irradiation on anthocyanin synthesis in cabbage seedlings. Anthocyanins were extracted 48 hr after the beginning of the light treatments. The absorbance values reported in the figure were corrected by subtracting the value of the dark controls. The first number in each bar is the length of the irradiation, in sec, in each 1-min cycle; the second number is the irradiance in μw cm^{-2}. S.D.: standard deviation.

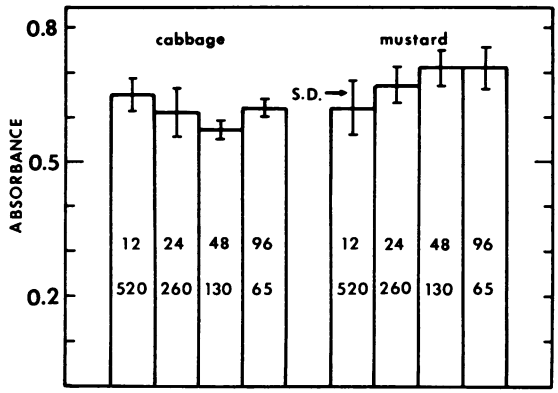

FIG. 4. Action of cyclic FR irradiation on the synthesis of anthocyanins in cabbage and mustard seedlings. Anthocyanins were extracted 48 hr after the beginning of the irradiation. The absorbance values given in the figure were corrected by subtracting the values of the dark controls. S.D.: standard deviation. The first number (top) in each bar is the length of the irradiation, in sec, in each 6-min cycle; the second number is the irradiance in μw cm^{-2}. Total radiation dose: 3 joules cm^{-2}.

Table II. *Effect of Cycle Length on Anthocyanin Synthesis in Cabbage and Mustard Seedlings*

Anthocyanins were extracted 48 hr after the beginning of the light treatments. The absorbance values reported in the table were corrected by subtracting the absorbance values of the dark controls. Light treatment was the length of irradiation in each cycle per length of the cycle. Irradiance of the FR source was 520 μw cm^{-2}. Total radiation dose was 18 joules cm^{-2}.

Light Treatments	Absorbance	
	Cabbage	Mustard
2 sec/10 sec	1.20	1.11
12 sec/60 sec	1.24	1.13
24 sec/120 sec	1.11	1.16
72 sec/360 sec	1.04	0.91
144 sec/720 sec	0.85	0.82
360 sec/1800 sec	0.61	0.57

from 1 min to 30 min reduces the level of anthocyanin accumulation about 50%. The $t_{0.5}$ for Pfr decay in mustard seedlings is about 30 min (14).

DISCUSSION

Intermittent FR treatments with short dark intervals between successive irradiations are as effective as continuous ones, if the total radiation doses applied with the two types of treatments are equal and are applied over equally long periods of time. Under cyclic FR treatments, the level of anthocyanin accumulation is not irradiance dependent, as it is under continuous irradiation, but dose ($t \times I$) dependent (Figs. 3 and 4). It may be possible that the observed irradiance dependence of the HIR (14, 22) is only an aspect of the dose dependence, the only aspect that can be observed under continuous irradiations. Under cyclic FR treatments, reciprocity relationships are valid (Figs. 2, 3, and 4). The validity of the reciprocity relationships for HIR anthocyanin synthesis under cyclic FR would indicate that cooperative phenomena between two different photoreceptors do not take place or are minimal.

The high effectiveness, the dose dependence, and the validity of the reciprocity relationships for HIR anthocyanin syn-

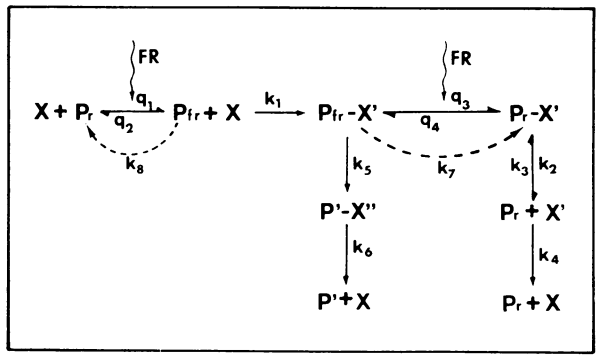

FIG. 5. A simplified model for phytochrome action in HIR responses under FR. P': nonreversible phytochrome; X: receptor site in the conformation existing before binding (high affinity for Pfr, low affinity for Pr); X': receptor site in the conformation existing after binding to Pfr (increased affinity for Pr; $t_{0.5}$ for X' to X = about 1 hr); X": receptor site in the conformation existing when bound to P' ($t_{0.5}$ for X" to X = several hr); k = rate constants; q: $\epsilon\phi$ (extinction coefficient × quantum efficiency). (This model is based on data from the following references: 1, 2, 3, 12, 15–18.)

thesis under cyclic FR treatments do not support the hypotheses of cycling between Pr and Pfr and formation of Pfr* as an explanation for the irradiance dependence and the reciprocity failure of the HIR, at least not in their present formulation (7, 14, 21); the rate of cycling between Pr and Pfr and the photostationary concentration of Pfr* are a function of irradiance (14, 22).

Because the results submitted with this report do not offer much support for the Pfr* hypothesis, and results submitted previously (10, 11) do not offer much support for an involvement of photosynthesis in the HIR responses of young seedlings, we are left with the task of providing another hypothesis for the irradiance (dose) dependence of P action in HIR responses. The hypothesis should satisfy the irradiance (dose) dependence of the HIR and should not require the involvement of either Pfr* or photosynthesis.

The situation of the P system in seedlings exposed to continuous or cyclic FR might possibly be represented by the model of Figure 5. The model is based on current ideas on the mechanism of action of P (8, 14, 22), on a model for P action in HIR responses proposed by Borthwick *et al.* in 1968 (2), and on recent findings on the binding of P to a particulate fraction (1, 12, 13, 15–18). A feature common to current models on the mechanism of action of P is that Pfr reacts with a partner X, and the products of the action of PfrX lead to the observed physiological responses. Pfr is the physiologically active form of P, and PfrX would be the intermediate effector. Results on the binding of P to a particulate fraction (1, 12, 13, 15–18) have shown that: (*a*) very little P becomes bound in darkness; (*b*) R enhances P binding (Pfr-bound); (*c*) Pfr enhances the sensitivity of the binding site (X) for Pr binding, so that the level of P bound after a R-FR sequence is higher than in darkness or after FR only, and can be even higher than the level bound after R; (*d*) the binding reaction results in conformational changes of the receptor sites (X→→→X'; X→→→X'→→ →X"); (*e*) the rate of irreversible decay (loss of spectrophotometrically detectable P) of membrane-bound Pfr is higher than that of unbound (soluble) Pfr; (*f*) the rate of the Pfr + X→→→Pfr-X' reaction is much faster than the rates of the Pfr-X'→→→P' + X and Pfr-X'→→→Pr + X overall reactions; and (*g*) the binding reaction is a function of the total number of Pfr molecules formed during the irradiation period. The model of Figure 5 does not include terms for the *de novo* synthesis of P and X and for the physiological action of Pfr-'X; these omissions are attributable to our desire to keep the model as simple as possible. The essential features of the model are the following: Pfr becomes bound very quickly after being formed; the binding and the reactions after it result in a decrease of the concentrations of X and soluble P, and in an increase of the affinity of the receptor site for Pr. The concentrations of the various components of the model at any given time are a complex function of the various reactions, as shown by the following equations:

$$d[\text{Pfr}]/dt = Iq_1[\text{Pr}] - Iq_2[\text{Pfr}] - k_1[\text{Pfr}][\text{X}] - k_8[\text{Pfr}] \quad (1)$$

$$d[\text{Pfr-X}']/dt = k_1[\text{Pfr}][\text{X}] + Iq_4[\text{Pr-X}'] - (Iq_3 + k_7 + k_5)[\text{Pfr-X}'] \quad (2)$$

$$d[\text{Pr-X}']/dt = (Iq_3 + k_7)[\text{Pfr-X}'] + k_3[\text{Pr}][\text{X}'] - (Iq_4 + k_2)[\text{Pr-X}'] \quad (3)$$

$$d[\text{X}]/dt = k_6[\text{P'-X}''] + k_4[\text{X}'] - k_1[\text{Pfr}][\text{X}] \quad (4)$$

No substitutions have been operated in the above equations, but it is quite evident that the rate of each single reaction is a function of the reactions before and following it. The terms in k_7 and k_8 are probably negligible under continuous irradiations or cyclic ones with short dark intervals between successive exposures, since the rate of dark reversion is much slower than the rate of photochemical turnover. The term in k_7 may become important when the length of the dark intervals between successive irradiations is increased. The term in k_8 should become important only when the concentration of X is negligible and the dark intervals between successive irradiations are long. The model and the equations derived from the model satisfy the irradiance (dose) dependence of the HIR, since the Pfr/P photoequilibrium ratio and the steady state concentration of Pfr-X' can become irradiance independent only if the contribution of several nonphotochemical reactions becomes negligible, an assumption not supported by the data presently available on P binding. It has been shown that the rate of formation of Pfr-X' is very fast, and that the concentration of X does not seem to be a limiting factor. In addition, after prolonged periods of exposure, the terms in k_2, k_3, k_4, k_5, and k_6 may become important for their effects on the concentrations of free X and soluble P and, consequently, on the rate of formation and the concentration of Pfr-X'. The validity of the reciprocity relationships for anthocyanin synthesis under cyclic FR (Figs. 3 and 4) can be explained on the basis of the model, because the concentration of the Pfr-X' complex is a function of the total number of Pfr molecules formed. The fact that a short R, applied after a prolonged FR irradiation, enhances anthocyanin accumulation (Table I; Fig. 1) can also be explained according to the model, because a terminal R irradiation increases the Pfr/P ratio and, consequently, the concentration of Pfr and of Pfr-X'.

The irradiance dependence of the HIR might be explained as a consequence of the necessity to maintain a certain minimum concentration of Pfr-X', necessary for the expression of the response under conditions of decreasing levels of free X and soluble P, of increasing competition between Pr and Pfr for the binding sites, and of increasing levels of the P'-X" and Pr-X' complexes.

One of the advantages of the proposed model is that it deals with components that can be subjected to direct measurements: Pr, Pfr, P decay, P binding as Pfr or Pr or both, changes in the level of the binding structure. At the same time, it should not be overlooked that the model of Figure 5 is based on several assumptions: (*a*) that the expression of P-mediated responses involves the formation of a PfrX complex; (*b*) that the binding of P to a particulate fraction is a specific, well-defined reaction; and (*c*) that the particular type of binding reaction studied so far is important in relation to the particular response studied, in our case HIR anthocyanin synthesis. The first assumption, *a*, is fundamental to all the models proposed to explain the mechanism of action of P and is supported, in a general way, by the

results obtained in P research (see refs. 8, 14, 22 for a general review). The other two assumptions, *b* and *c*, while reasonable, have not yet been definitively proven.

The results reported in this note support the hypothesis that P is the only photoreceptor involved in HIR anthocyanin synthesis of young seedlings exposed to FR radiation. Experiments are currently in progress in our laboratory to determine if the measurable changes of various components of the model under continuous and cyclic FR irradiations agree with the physiological results obtained for HIR anthocyanin synthesis in cabbage seedlings. Other experiments are also in progress to determine if the reciprocity relationships are valid for cyclic treatments with radiation in spectral regions other than FR.

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