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Photomorphogenesis in Sinningia speciosa, cv. Queen Victoria[1] I. Characterization of Phytochrome Control

Ruth L. Satter[2] and Donald F. Wetherell
University of Connecticut, Storrs, Connecticut 06268

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Abstract. **The morphological development of *Sinningia speciosa* plants that were exposed to supplementary far red light was very different from that of plants receiving dark nights. After several nights of such irradiation, stems and petioles were elongated, petioles were angulated, leaf blade expansion was inhibited, plants were chlorotic and the accumulation of shoot dry weight was retarded.**

Red reversibility of the morphological changes potentiated by far red light indicated control by the phytochrome system. A high P_{FR} level during the last half of the night inhibited stem elongation and promoted leaf blade expansion, but both of these processes were hardly affected by the P_{FR} level during the first half of the night. Thus sensitivity to P_{FR} was cyclic.

The interpretation of our experiments was complicated by quantitative morphological differences resulting from long, as compared to short, far red irradiations.

When *Sinningia speciosa* plants were irradiated by fluorescent light of photosynthetic intensity for 8 hours daily and by a far red source for several hours each night, stems and petioles elongated, leaf blades failed to expand normally, petioles became angulated, and chlorosis developed. This contrasted sharply with the short, thick stems and large, horizontal leaf blades of controls receiving dark nights. Some of these phenomena have been noted in other species and been attributed to the effect of the light source upon the phytochrome[3] system (6, 8, 12, 13, 22). Our preliminary experiments implicated phytochrome as a regulatory mechanism in *Sinningia*, too, since morphological changes potentiated by far red could be reversed by red. These experiments, however, gave some unexpected and perplexing results that revealed the complex nature of phytochrome control in *Sinningia*. 1) Morphological development was controlled by the P_{FR} level during a few critical hours, but was almost independent of its level during the remainder of the night. 2) The effects of far red light were dependent upon the duration of the irradiation. 3) When plants were irradiated for several hours during the last half of the night, elongation was maximized by sources that emitted red and far red rather than far red alone. [See Part II of this series (21)].

Materials and Methods

Plant Materials. *Sinningia speciosa* cv. Queen Victoria plants were grown from seed obtained from self-pollinated stock plants maintained in our greenhouse. They were 6 to 12 weeks old when experiments began. The initial seed came from Geo. W. Park Seed Company.

Experimental Conditions. Experiments were conducted in 2 growth chambers illuminated for 8 hours each day by a combination (2:2:1) of Sylvania cool white, warm white, and Gro-lux fluorescent lamps. Illuminance was 1150 ft-c in Chamber No. 1 and 900 ft-c in Chamber No. 2. Temperature (25° ± 1° during the day and 21° ± 1° at night) and relative humidity (60 %) was the same in both chambers.

Individual experiments continued for 14 to 21 days. Light treatments during this period consisted of supplementary irradiation during part or all of the 16 hour night.

Plants from Growth Chamber No. 1 were moved to incubators for their supplementary light treatments. Incubators were equipped with the following light sources: A) incandescent source: 7 watt bulbs, whose radiation was filtered through 2 inches of water. B) Far red source: same as A), but also filtered by far red plexiglas (FRF700, one-eighth in. thick, Westlakes Plastic). This filter absorbs virtually all radiation below 700 mμ, and established a P_{FR} level of 1 % to 3 % in etiolated *Avena* seedlings (18). C) Unfiltered fluorescent source: 15 watt cool white tubes. D) Red source: same as C), but covered with 3 layers of red cellophane (Dupont).

Growth Chamber No. 2 was divided into 3 light-proof sections each containing its own supplementary

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[2] Present address: Department of Biology, Yale University, New Haven, Connecticut.

[3] The designations P_{FR} and P_R will be used throughout to indicate the far red and red absorbing forms of phytochrome.

red and far red sources in vertical banks at opposite ends of the plant bench and 15 inches above plant level. Lamps and filters were similar to those used in the incubators, except the incandescent bulbs were of higher wattage (25, 50, or 75 w). Water in the filters was circulated to prevent overheating. The lamps in each bank were spaced to provide uniform intensity along rows of plants parallel to the surface of the bank.

Light Measurement. Illuminance from the photosynthetic sources was measured with a Weston meter. Irradiance from supplementary sources was measured with a Densichron meter (Welsh Scientific Co.) containing a photocell with peak sensitivity at 800 mμ. The spatial relationship between the probe and the light sources influences light measurements. We used a detecting probe covered with a translucent hemisphere to mitigate this problem. The probe position was kept horizontal for all measurements. This most closely approximated the geometrical relationship between the light sources and the plants' absorbing surfaces at the beginning of an experiment. However, it should be noted that leaf angles change during the course of an experiment.

The Densichron was calibrated against a standardized Eppley linear thermopile for each source used. The red and far red spectral regions were isolated for measurement purposes at both Densichron and thermopile windows by narrow band pass interference filters (Eppley, WL 655 mμ, T65 %, HW 12 mμ and WL731 mμ, T29 %, HW 17 mμ). Radiant flux density of the broader regions most active in phytochrome reactions (2, 14, 25), 600 to 700 mμ and 700 to 780 mμ, was calculated using these measurements, manufacturers' lamp spectral data, and measured filter transmission data.

Energy dosage studies indicated that exposure of *Sinningia* plants to 45 mjoule in the far red region and 40 mjoule in the red region, saturated the effect of a short far red irradiation and its red reversal.

Interpretation of Data. Light treatments were given to groups of 9 to 12 uniform plants. Controls receiving a dark night were included in most experiments.

The following parameters were measured: Stem elongation was measured from the upper edge of the first node to that of the third or fourth node. Height data include standard deviation (SD). The second youngest expanded leaf pair was chosen for measurement of blade/petiole ratio, petiole angle and chlorophyll content. Blade length was measured along the central midrib. Petiole angle was measured with a horizontal line as base. Dry weight of shoots was measured after drying for 24 or more hours at 85°. Chlorophyll was extracted by a modification of the method of MacKinney (17). Four discs of blade tissue, 0.58 cm in diameter, were removed from the region between the third and fourth lateral veins of the leaf pair, and were shaken in a vial with 4 ml of 80 % acetone. Vials were stored at −10° in darkness for 3 to 4 days. OD at 663 mμ was measured at room temperature.

Results and Discussion

Growth With Supplementary Red or Far Red Irradiation. Plants grown with a dark night had short stems, large leaf blades with short horizontal petioles, lateral branches and high chlorophyll content. Leaf blades were slightly crinkled, since veins were short relative to the expansion of the lamina.

Table I. *Effects of 16 Hours of Supplementary Irradiation on* Sinningia speciosa

Plants were grown on 8 hour photoperiods of fluorescent light at 1150 ft-c. Supplementary light treatments were continued for 15 nights. Height data include SD. Percentage data refer to dark control.

	Dark	Far red[1]	Fluorescent[1]
Stem height (cm)[2]	0.81 ± 0.04	2.83 ± 0.42	0.83 ± 0.04
		350 %	103 %
Blade length/petiole length[3]	7.6	3.5	9.8
		46 %	129 %
Petiole angle (deg)[4]	15	71	12
OD 663 mμ of leaf extract[3]	0.57	0.34	0.72
		60 %	126 %
Shoot dry wt (mg)	290	151	319
		52 %	110 %
Shoot growth (mg dry wt)[5]	224	85	253
		38 %	113 %
Leaf dry wt (mg)[3]			
Blade	45.5	12.5	64.7
Vein	14.1	9.2	19.6
Blade/vein	3.2	1.4	3.3

[1] Far red irradiance of 77 μw cm^{-2} (700–780 mμ). Fluorescent source is cool white, illuminance of 75 ft-c.
[2] Measured from first to fourth node.
[3] Fourth leaf pair, except single leaf for dry wt data.
[4] Angle between petiole and horizontal.
[5] Dry wt = 66 mg at zero time.

FIG. 1. Plants that were irradiated by far red light or cool white fluorescent light for 16 hours each night, for 15 consecutive nights, are shown together with their control that received dark nights (see table I for measurements). Left to right: far red light, fluorescent light, dark.

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However, if plants received far red radiation during the night, stems and petioles elongated considerably, leaf blade expansion was inhibited, petioles approached a vertical position, chlorophyll content and dry weight were reduced, and growth exhibited apical dominance. Leaves curled under, because vein elongation exceeded expansion of the lamina, causing deforming mechanical stresses.

Plants that received low intensity red light or unfiltered cool white fluorescent light during the night, resembled the dark controls in general growth habit, but had more chlorophyll and a higher dry weight (table I and fig 1).

Changes caused by far red light were detectable after 2 or 3 nightly irradiations. They rapidly became more severe as light treatments were continued. Leaves whose growth had been severely inhibited by many such treatments failed to develop normally even after irradiations were discontinued, although newly formed leaves and stems responded immediately to changed conditions.

Although stem elongation induced by far red radiation has been correlated with promotion of flowering in a number of plants (7, 22) this is not the case in *Sinningia.*

Phytochrome Mediation. Regulation by phytochrome was demonstrated as follows: 1) Morphological changes were measurable at very low irradiance (0.5 μw cm^{-2} between 700–780 mμ). 2) Physiological changes induced by far red light were prevented if short far red treatments were immediately followed by red treatments (table II).

Thus growth changes arising from far red irradiation were caused, at least in part, by a low P_{FR} level. When a high P_{FR} level was maintained by supplementary white fluorescent or red light, plants were similar in most respects to controls receiving dark nights; differences in chlorophyll, leaf blade size, and weight gain (table I) were investigated further, and found to be due to a photosystem other than phytochrome (21).

It is interesting to note that reversion of P_{FR} to P_R in *Sinningia* is slow. Plants grown with dark nights that were interrupted by a short light break at the twelfth hour, resembled controls if the light break was red, but elongated if the light break was far red. Stable P_{FR} has been reported for a variety of plants (5, 8, 12).

We interpret the data of tables I and II as follows: leaf blade expansion and inhibition of stem elongation both require a high P_{FR} level (6, 8, 22). Chlorophyll content is also regulated by phytochrome (12, 13). It is quite likely that a low P_{FR} level during the night impedes chloroplast development in *Sinningia,* since this condition has been shown to inhibit structural development of the bean plastid (16, 20). However, we feel that phytochrome control of chlorophyll level in our material is primarily indirect, *i.e.* it results from a deficiency of substrate which, in turn, arises from reduced photosynthetic capacity. Reduced ratios of photosynthetic to non-photosynthetic tissue, and the change in blade orientation from horizontal to nearly vertical, result from a low P_{FR} level, and are major contributory factors.

The cumulative nature of these processes brings about a dramatic change in the appearance of far red-treated plants. The cyclic processes of reduction in photosynthetic area followed by reduced pigmentation which further reduces photosynthetic capacity leads rapidly to severe chlorosis and stunting.

Inhibition of chlorophyll synthesis (9, 26) enhancement of its destruction (10, 24) and prevention of normal structural development of the chloroplast (9) in other species have all been reported as resulting from substrate shortages.

Cyclic Sensitivity to Far Red Light. Morphological changes were most pronounced when far red irradiations were given during the last 8 hours of the night (table III). The P_{FR} level during the first half of the night proved to be relatively unimportant (table IV). This was further demonstrated

Table II. *Reversibility by Red Light of the Effects of Far Red Light on* Sinningia speciosa

Plants were grown on 8 hour photoperiods of fluorescent light at 1150 ft-c. Supplementary light treatments were continued for 15 nights. Height data include SD. Percentage data refer to dark control.

	Dark	Pulses of far red[1]	Pulses of far red, red[1]
Stem height (cm)[2]	0.78 ± 0.08	1.70 ± 0.24	0.76 ± 0.06
		218 %	97 %
Blade length/petiole length[3]	5.9	3.5	7.5
		59 %	127 %
Petiole angle (deg)[4]	21	55	19
OD 663 mμ of leaf extract[3]	0.52	0.35	0.54
		67 %	104 %
Shoot dry wt (mg)	254	185	322
		73 %	127 %

[1] Far red pulse length = 100 sec. Red pulse length = 120 sec. Pulses repeated every 20 minutes during the 16 hour night. Far red irradiance = 40 μw cm^{-2} (700–780 mμ). Red irradiance = 137 μw cm^{-2} (600–700 mμ).

[2] Measured from first to fourth node.

[3] Third leaf pair, counted from base of stem.

[4] Angle between petiole and horizontal.

in a related experiment in which plants receiving 15 minutes of far red irradiation at the middle of the night were nearly as tall as those irradiated for the first 8 hours of the night.

In another experiment, the period of maximum sensitivity to phytochrome was further defined when plants received a short far red irradiation reversed by a short red treatment 4 hours later. These light treatments were given for 17 consecutive nights. Stem height was 158 % of the control value when P_{FR} was low during the last quarter of the night. This compares with 122 % when P_{FR} was low during the third quarter of the night.

In another experiment reported in table V, we found that *Sinningia's* far red sensitivity during the second half of the night was nearly obliterated by exposure during the first 8 hours of the night to a red-containing source. This red light effect was intensity dependent. (Compare the effects of the red treatment in table IV with that of the fluorescent treatment in table V).

Thus, promotion of leaf blade expansion and inhibition of elongation both require a high P_{FR} level during the last period of the night. These processes are almost independent of the P_{FR} level during the first half of the night, somewhat sensitive to the level during the third quarter, and largely determined by the level during the last quarter. Red light during the first half of the night reduces subsequent phytochrome control.

Sinningia's sensitivity to P_{FR} is cyclic. It contrasts with that of Pinto bean, whose elongation

Table III. *Response of* Sinningia speciosa *to Far Red Irradiation Given During the First Compared to the Second Half of the Night*

Plants were grown on 8 hour photoperiods of fluorescent light at 1150 ft-c. Supplementary light treatments were continued for 14 nights. Height data include SD. Percentage data refer to dark control.

	Dark	Dark (8 hr) Far red[1] (8 hr)	Far red[1] (8 hr) Dark (8 hr)
Stem height (cm)[2]	0.71 ± 0.06	2.15 ± 0.39	1.50 ± 0.30
		303 %	212 %
Blade length/petiole length[3]	3.9	2.6	2.7
		67 %	70 %
Petiole angle (deg)[4]	20	73	68
OD 663 mμ of leaf extract[3]	0.48	0.29	0.27
		60 %	56 %
Shoot dry wt (mg)	206	149	142
		72 %	69 %

[1] 28 μw cm^{-2} (700–780 mμ).
[2] Measured from first to fourth node.
[3] Third leaf pair, counted from base of stem.
[4] Angle between petiole and horizontal.

Table IV. *Responses of* Sinningia speciosa *to Several Irradiation Sequences*

Plants were grown on an 8 hour photoperiod of fluorescent light at 1150 ft-c. Supplementary light treatments were continued for 17 nights. Height data include SD. Percentage data refer to dark control.

	Dark (D)	Fr[1] (8 hr) R[4] (one-half hr) D (7 and one-half hr)	Dark (8 hr) Inc[3] (8 hr)	Red[2] (8 hr) Inc[3] (8 hr)	Inc[3] (16 hr)	Fr[1] (8 hr) Inc[3] (8 hr)
Stem height (cm)[5]	0.52 ± 0.08	0.62 ± 0.05	2.06 ± 0.25	1.92 ± 0.32	1.85 ± 0.35	2.04 ± 0.22
		119%	396 %	369 %	356 %	392 %
Blade length[6]	5.5	3.5	2.5	2.8	2.5	2.1
Petiole length		64 %	45 %	51 %	45 %	38 %
Petiole angle (deg)[7]	2	15	38	34	37	45
Shoot dry wt (mg)	158	145	145	152	154	122
		92 %	92 %	96 %	97 %	77 %

[1] 39 μw cm^{-2} (700–780 mμ).
[2] 10 μw cm^{-2} (600–700 mμ).
[3] 58 μw cm^{-2} (600–700 mμ) and 54 μw cm (700–780 mμ).
[4] 72 μw cm^{-2} (600–700 mμ).
[5] Measured from first to fourth node.
[6] Third leaf pair, counted from base of stem.
[7] Angle between petiole and horizontal.

Table V. *The Effect of Fluorescent Irradiation During the First Half of the Night on the Response of* Sinningia speciosa *to Subsequent Far Red Irradiation*

Plants were grown on an 8 hour photoperiod of fluorescent light at 1150 ftc. Supplementary light treatments were continued for 17 nights. Height data include SD. Percentage data refer to dark control.

	Dark	Dark (8 hr) Far red (8 hr)	Fluorescent[1] (8 hr) Far red[1] (8 hr)
Stem height (cm)[2]	0.42 ± 0.02	1.03 ± 0.30	0.51 ± 0.15
		245 %	121 %
Blade length/petiole length[3]	6.4	3.3	4.5
		52 %	70 %
Petiole angle (deg)[4]	15	49	33
Shoot dry wt (mg)	82	52	74
		63 %	90 %

[1] Far red irradiance of 38 μw cm^{-2} (700–780 mμ). Fluorescent source is cool white, irradiance of 95 μw cm^{-2} (600–700 mμ) and illuminance of 80 ft-c.
[2] Measured from first to third node.
[3] Second leaf pair, counted from base of stem.
[4] Angle between petiole and horizontal.

Table VI. *The Response of* Sinningia speciosa *to a Short Far Red or Incandescent Irradiation in the Middle of the Night as Compared to Long Irradiation during the Last Half of the Night*

Plants were grown on an 8 hour photoperiod of fluorescent light at 1150 ft-c. Supplementary light treatments were continued for 20 nights. Height data include SD. Percentage data refer to dark control.

	Dark (D)	D (8 hr) Fr[1] (1 hr) D (7 hr)	D (8 hr) FR[2] (8 hr)	D (8 hr) Inc[3] (1 hr) D (7 hr)	D (8 hr) Inc[4] (8 hr)
Stem height (cm)[5]	0.67 ± 0.07	1.05 ± 0.19	1.46 ± 0.46	0.69 ± 0.08	2.29 ± 0.47
		157 %	218 %	103 %	342 %
OD 663 mμ of leaf extracts	0.50	0.40	0.26	0.40	0.46
		80 %	52 %	80 %	92 %
Shoot dry wt (mg)	204	162	143	167	176
		79 %	70 %	82 %	86 %

[1] 77 μw cm^{-2} (700–780 mμ).
[2] 46 μw cm^{-2} (700–780 mμ).
[3] 58 μw cm^{-2} (600–700 mμ) and 54 μw cm^{-2} (700–780 mμ).
[4] 36 μw cm^{-2} (600–700 mμ) and 33 μw cm^{-2} (700–780 mμ).
[5] Measured from first to fourth node.
[6] Third leaf pair, counted from base of stem.

appears to be controlled by P_{FR} during all parts of the night (8). Cyclic sensitivity to phytochrome has, however, been demonstrated in the flowering response of a number of species (1, 4, 5, 11, 23). Also, phase shifts caused by red light have been observed for many rhythmic processes (3).

Comparison of The Effects of Long and Short Far Red Irradiations. When plants were exposed to far red light during the second half of the night, the following were noted (table VI): 1) Plants were taller, had smaller leaves, less chlorophyll, and showed less dry weight accumulation when exposures were 8 hours of far red light rather than 1 hour followed by 7 hours of darkness. 2) Disparity in response to long compared to short irradiation was particularly pronounced when the source was incandescent light filtered only by water. Then short irradiations had no effect upon elongation, although 8 hour exposures produced plants taller than those irradiated by a well filtered far red source. The latter data are discussed in (21).

The effect of pulsed irradiation was tested. Morphological changes were as severe as with continuous irradiation if the pulses were repeated every 30 minutes. However, the same total energy was less effective when given in pulses separated by dark intervals of 90 or more minutes.

The effect of irradiance was also tested. When plants received a short far red irradiation in the middle of the night followed by 8 hour exposures to far red light of different intensities, the time-dependence of morphological changes was saturated by an irradiance of 9 μw cm^{-2} (700–780 mμ). This low saturation energy suggests that phytochrome is the only photoreceptor involved.

Two explanations of the observed time-dependence have been considered and rejected. If phytochrome was synthesized during the second half of the night, in the P_{FR} form, a long or a pulsed far red irradiation would be required to maintain a low P_{FR} concentration. Synthesis has been measured in many species but always in the P_R form (15).

The possibility that intermediates of phytochrome photoconversion control the phenomena we have

described, seems unlikely because the rate of intermediate formation is intensity dependent and very low intensities were saturating in our experiments.

Mancinelli *et al.* (19) have described another phytochrome-controlled process that showed a similar irradiation dependence. Continuous or pulsed far red light was required for maximum inhibition of Porte tomato seed germination.

Conclusion

Pronounced morphological changes arise when *Sinningia* plants are irradiated with far red light during a 16 hour night. Sensitivity to this irradiation is variable and reaches a peak during the last half of the night. This cyclic sensitivity can be altered if red light of sufficient intensity is given early in the night.

These photomorphogenic responses are controlled by phytochrome. However, the unequal effects of long and short far red treatments cannot be explained in terms of known phytochrome physiology.

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