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Characterization of the Light Reaction in Promoting the Mobilizing Ability of Rose Shoot Tips[1]

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ABSTRACT

Mixed fluorescent and incandescent light increased growth and sink strength of the uppermost young shoot of rose plants (*Rosa hybrida* cv. Marimba) in comparison to pure fluorescent light. This was manifested by increased apical dominance. Monochromatic low-energy red light, given by means of optic fibers for 24 hours to shoot tips that had been previously darkened for 5 days, increased the transport of ^{14}C-labeled assimilates to the intact tips and the uptake of [^{14}C]sucrose by detached tips. Far-red had little or no effect, and blue was not effective at all in these reactions. Red light given directly to detached shoot tips, *in vitro*, increased the uptake of [^{14}C]sucrose by the isolated tips. Adding far-red to the red greatly promoted the uptake, whereas blue and blue plus far-red were not active. The main character of the light reaction promoting sink activity in the shoot is that it is perceived by the shoot tip itself. It is operated by red light; far-red promotes the red effect but has little or no effect when alone. Light apparently promotes shoot sink activity by increasing the unloading process.

Light has a promotive effect on translocation of assimilates to vegetative (16) and reproductive (9, 11) sinks. It has also been shown that uptake of [^{14}C]sucrose by detached pea epicotyls was greatly enhanced by R[3] and inhibited by FR light (20). This effect preceded the growth response to light. Previous work on roses (11) showed that darkening of only young shoot, while other parts of the plant were exposed to high-intensity light, greatly reduced the translocation of ^{14}C-labeled assimilates to the darkened shoot tip and had a detrimental effect on growth and flowering of the darkened shoot. The decrease in translocation was detected prior to flower atrophy. This light effect was independent of photosynthesis and probably also of ATP formation.

The purpose of this study was to define the character of this reaction by using light from different sources and at different spectral composition.

MATERIALS AND METHODS

Plants. Four- to five-month-old plants of *Rosa hybrida* cv. Marimba were raised from own rooted (ungrafted) cuttings. Only one flowering stem was left on each plant. It was decapitated prior to each experiment on the second five-leaflet leaf, counting from the distal end of the stem (Fig. 2). After bud breaking, the upper buds were allowed to develop into new young shoots and the rest removed. Usually, the uppermost shoot was used for the experiment.

Experiments in which the young shoot was darkened started 9 to 10 days after decapitation, when the young shoot had reached the length of 3 cm. In other experiments, the growth stage is given with the results. Other details concerning growth conditions and preparation of plants for the experiments have been described elsewhere (10, 11).

Growth Chambers. Two similar growth chambers were used for the experiments with conditions as described previously (11). Details of specific experiments are presented with the results.

Light Conditions. In experiments with Fl and mixed Fl and In light, the irradiance energy in both chambers was about 50 w m^2 at the top of the plants, as measured with model LI 185-A Lambda light meter (Lambda Instrument Corp.). In one chamber, all light was from cool white Fl lamps and in the second, 50% was from In bulbs. The spectral energy in the chamber with Fl light was 3.7, 2.4 and less than 0.5 μw cm^{-2} nm^{-1} in B, R, and FR, respectively, and, in the chamber with mixed Fl and In light, spectral energy was 2.7, 4.2, and 3.8 μw cm^{-2} nm^{-1} in B, R, and FR, respectively.

Optic glass fibers (Shott-Mainz, Germany), were used to supply narrow-beam, monochromatic light. The fibers were 80 cm long and were attached to a common light source (Fig. 1). The appropriate spectrum was obtained by using 660-nm R filter, and 728-nm FR filter (half-band width, 20 nm; Schott-Mainz), celluloid No. 1460 (Celluloid Fabrik, Speyer, Germany) with transmission in B and FR, and celluloid No. 1654 (Mazzuchelli, Castiglione, Olona, Varese, Italy) with transmission in B. In some experiments, R cellulose filter with transmission in R and FR (8) was used. Detailed spectrum curves of the celluloid filters have been presented elsewhere (6) and the light energy fluxes in the three colors are presented with the results (Tables III, IV, and V).

With the optic glass fibers, intermittent lighting of 75 s light and 150 s dark was used. This method was found to be more efficient than continuous light (13) and also prevented overheating of the light source.

Young rose shoots were enclosed in glass cylinders covered with black polyethylene and aluminum foil. The optic glass fiber was inserted through cork stopper in the upper end of the cylinder and was directed to the shoot tip by means of a rubber weight. C_2H_4-free air was passed through the cylinders during the experiment as described (11).

[^{14}C]Sucrose Uptake *in Vitro*. [^{14}C]Sucrose uptake was studied either by using a liquid medium technique (3) or by planting the shoot tip on agar (1). Shoot tips 4 mm long (or 5 mm for agar medium) were collected, and leaves which could be removed

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[3] Abbreviations: R, red; B, blue; Fl, fluorescent; FR, far-red; In, incandescent; RSA, relative specific activity.

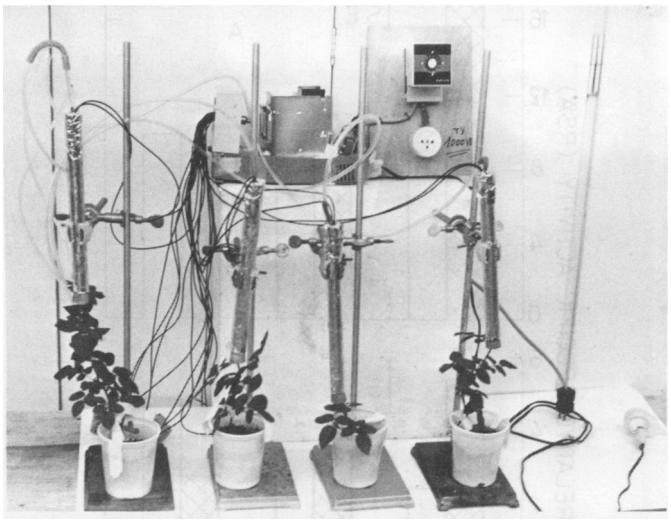

FIG. 1. Demonstration of lighting darkened rose shoot by narrow-beam monochromatic light, with optic fibers. The darkened shoot is enclosed in glass cylinders covered with black polyethylene and aluminum foil. Air is flown through the cylinder. The optic fiber enters the cylinder through a cork stopper and is placed directly on the tip.

without damaging the apex were peeled off. The tips were washed in distilled H_2O for 1 h. Labeled sucrose was purchased from the Radiochemical Centre, Amersham. The liquid incubation solution consisted of 5 mM [^{14}C]sucrose (0.24 mCi/mmol), 5 mM KH_2PO_4 (pH 5), and 0.5 M mannitol. One ml incubation solution was dispensed in 5-ml plastic vials and a shoot tip was added. After incubation for 3 h on a rotary shaker at 34 C in dim light, the shoot tips were washed three times, 15 min/wash, in chilled unlabeled incubation medium with 2 mM $CaCl_2$ added. Then the tips were frozen in liquid N_2, freeze-dried, weighed, ground with 1 ml distilled H_2O, and transferred to a scintillation vial to which 3 ml Aqua-Sol (New England Nuclear) was added. The vial was agitated to obtain a uniform gel. Each sample was counted for 2 min in a scintillation counter. Counting efficiencies were determined by the channel ratio method.

For [^{14}C]sucrose uptake from agar 5 mm long tips were planted in an agar-sucrose medium in 6-cm Petri dishes (5 ml medium/Petri dish). The agar-sucrose medium contained 3% labeled sucrose (7.8 μCi/mmol). The Petri dishes were covered with plastic lids and placed on wet filter paper, under glass beakers wrapped with appropriate light filters. The experiments were run in two growth chambers under continuous light. The light conditions are presented with the results.

The temperature in the Petri dishes, measured by thermocouples, was 24 C. After 48 h incubation, the 1.5 mm of the stem inserted in the agar was removed and the remaining portion of the shoot tip was weighed and transferred to a scintillation vial containing Bray's solution. The vials with individual tips were held for 24 h at room temperature and then frozen, thawed, and counted with scintillation counter.

Treatment with $^{14}CO_2$ and ^{14}C Detection. Pulsing with $^{14}CO_2$ and ^{14}C detection were as described before (10, 11). $^{14}CO_2$ was generated from 40 μCi $NaH^{14}CO_3$ (Radiochemical Centre, Amersham, England), diluted with 80 mM $NaHCO_3$ to final specific radioactivity of 1.25 mCi/mol, by injecting 0.5 ml 50% lactic acid through a rubber stopper planted in the lid of the plastic container in which the source leaf was enclosed.

The duration of the radioactive pulse was 1 h and the plants were harvested after the translocation period given with the results.

The radioactivity in the various plant parts was expressed as a percentage of the radioactivity recovered in the plant, excluding the source leaf, or as RSA, defined as the ratio of per cent radioactivity in a given plant part to dry weight of this part in per cent of total dry weight (11).

RESULTS

Effect of Fluorescent and Incandescent Lamps. Fourteen young rose plants were decapitated, divided into two groups of seven each, and transferred to two growth chambers which were illuminated either by Fl and In lamps (each about 50% of the light energy) or by Fl lamps only. The total light energy at the top of the plants was about 50 w/m^2 in both chambers. On day 6 after decapitation, the number of sprouted buds and their length were recorded. The two shoots which developed from the upper buds were retained, but their subtending leaves were removed. The plants stayed in the growth chamber for 6 more days. On day 12 after decapitation, four uniform plants were chosen from each treatment and $^{14}CO_2$ was given to a leaf one node below the second shoot. The length of the shoots was measured again, and the distribution of soluble radioactivity established, after a 4-h translocation period.

Plants grown under Fl light had significantly more sprouted buds than those grown under mixed Fl and In light of equal energy (Fig. 2; Table I). Growth rate of the uppermost shoot in Fl and In light was almost double that of those grown in Fl light, whereas growth of the second shoot was unaffected (Table I).

Soluble radioactivity recovered from the uppermost shoot of

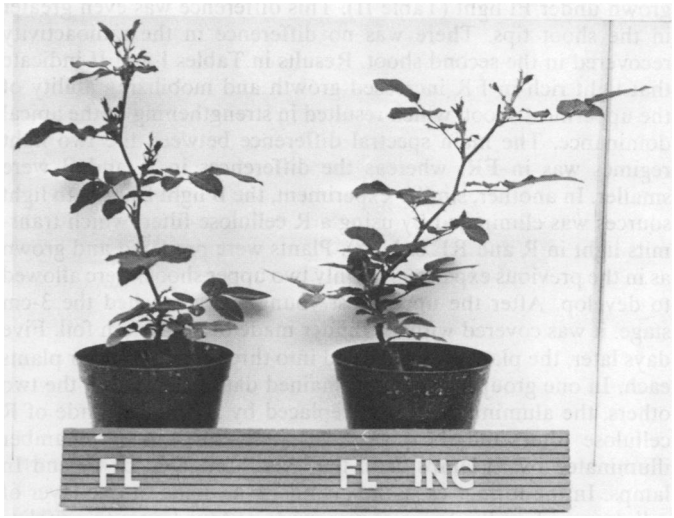

FIG. 2. The effect of pure Fl or mixed Fl and In light on axillary bud sprouting of rose plants (cv. Marimba). Four sprouted buds can be seen on the left plant (Fl), and only 2 can be seen on the right plant (mixed light).

Table I. *Sprouting and Length Increment from Days 6 to 12 after Decapitation of Young Rose Shoots Grown for 12 Days in Fluorescent or in Mixed Fluorescent and Incandescent Light (each 50% of Total Energy)*

Total light energy at plant level 50 w/m^2. The values are means of six plants.

Light Source	Number of Sprouted Buds	Length Increment	
		Uppermost Shoot	Second Shoot
		%	
Fl	3.6a[a]	37a	25a
Fl and In	2.3b	61b	21a

[a] Values followed by different letters within each column are significantly different at the 5% level (t test).

Table II. *Effect of Light Quality on Translocation of Labeled Assimilates from Common Source Leaf to Two Young Rose Shoots (cv. Marimba) Located on Same Branch*

Plants were grown under Fl or mixed Fl and In light (each 50% of total energy). Total light energy at plant level was 50 w/m^2. Twelve days after pruning, only the two upper young shoots were left and their subtending leaves were removed. Two days later, $^{14}CO_2$ pulse was given to the mature leaf on a node under the second young shoot. The translocation period was 4 h. The values are means of four replicates ± SE.

	Uppermost Shoot		Second Shoot	
	Methanol-soluble ^{14}C Translocated Out of Source	RSA	Methanol-soluble ^{14}C Translocated Out of Source	RSA
	%		%	
Whole Shoot				
Fl	48.1 ± 4.8	9.0 ± 1.6	14.8 ± 2.2	5.3 ± 1.1
Fl + In	56.6 ± 5.4	15.0 ± 2.4	15.4 ± 2.2	6.1 ± 1.3
Shoot tip				
Fl	2.5 ± 0.4	18.5 ± 3.4	0.9 ± 0.2	11.6 ± 1.4
Fl + In	4.2 ± 0.2	23.3 ± 1.9	1.1 ± 0.3	12.6 ± 4.1

plants grown under mixed light was greater than that of those grown under Fl light (Table II). This difference was even greater in the shoot tips. There was no difference in the radioactivity recovered in the second shoot. Results in Tables I and II indicate that light rich in FR increased growth and mobilizing ability of the uppermost shoot, which resulted in strengthening of the apical dominance. The main spectral difference between the two light regimes was in FR, whereas the differences in R and B were smaller. In another, similar experiment, the B light from both light sources was eliminated by using a R cellulose filter, which transmits light in R and RF only (8). Plants were prepared and grown as in the previous experiment. Only two upper shoots were allowed to develop. After the uppermost young shoot reached the 3-cm stage, it was covered with a cylinder made of aluminum foil. Five days later, the plants were divided into three groups of four plants each. In one group, the shoot remained darkened and, in the two others, the aluminum foil was replaced by a cylinder made of R cellulose filter, and the plants were left either in the chamber illuminated by Fl lamps or in the one illuminated by Fl and In lamps. In the former case, the cylinder was made of one layer of cellulose and, in the latter, it was made of four layers to equalize the light energy under the filter. Light energy flux was 3 and 3.4 μw cm^{-2} nm^{-1} in R and the mixed light, respectively. Light energy in the FR was nil under the Fl and 3.2 μw cm^{-2} nm^{-1} under the mixed light. After 30 h, $^{14}CO_2$ was given to a leaf one node below the second young shoot and, 18 h later, the plants were divided into parts and treated to determine the soluble radioactivity. Results are presented in Figure 3 in terms of RSA. They show that R light promoted the translocation of assimilates to the treated shoot tip. The addition of FR to the R doubled the promoting activity of the light.

Effect of Monochromatic Light on Mobilizing Ability of Shoot Tip. Two series of experiments were conducted. In the first, plants grown in a growth chamber were decapitated, and the new shoot (3 cm long), which sprouted from the uppermost axillary bud, was inserted into a glass cylinder covered with aluminum foil (Fig. 1). Five days later, five of the darkened shoot tips were illuminated by means of optic glass fibers with R, FR, or B monochromatic light for 48 h. In each experiment, two control groups were included: dark and full light. Thirty h after the beginning of the light treatment, $^{14}CO_2$ was given to a leaf one node below the treated shoot. Eighteen h later, the plants were divided into parts

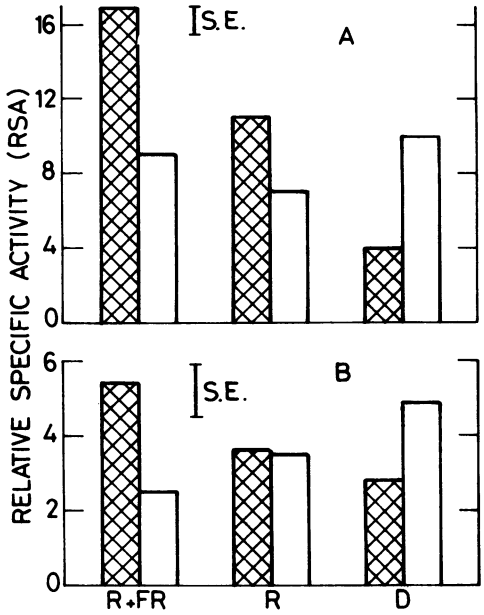

FIG. 3. Effect of R + FR on translocation of ^{14}C to a young rose shoot and its tip, after 5 days of darkening and to the untreated shoot below. Data presented as RSA. Young rose shoots that sprouted from the uppermost axillary bud on pruned branch were darkened 9 days after pruning for 5 days and then divided into three groups: one was the dark control (D) and, in the two others, the aluminum cap was replaced by R cellulose filter. One of the latter two groups was held under fluorescent (R) and the other was held under Fl and In light (R + FR) for an additional 48 h. $^{14}CO_2$ pulse was given 30 h after starting the light treatment. A, shoot tip; B, whole shoot. ■, uppermost treated shoot; □, second shoot below. The values are means of four treatments.

and the radioactivity was determined (Table III). In the second series of experiments, the plants were not pulsed and, instead, the shoot tips were illuminated *in situ* for 48 h after being darkened. The shoot tips were excised and incubated for 3 h in [^{14}C]sucrose solution (Table IV).

Lighting tips of darkened shoots with a low energy beam of monochromatic R light increased the radioactivity recovered in the tip to the level of an undarkened control (Table III). FR was also promotive, but to a lesser extent. Blue light had no effect. The difference between FR and R was even more pronounced in the [^{14}C]sucrose uptake by isolated tips (Table IV). In this case, FR and B treatments did not differ from their respective dark control, whereas R doubled the uptake of sucrose in comparison to the dark and reached 50% of the full light control, having more than a 22-fold higher light energy.

Effect of Colored Light on [^{14}C]Sucrose Uptake of Isolated Shoot Tips. Young shoot tips grown in full light were harvested 14 days after decapitation (5 days after reaching the 3-cm stage) and planted on Petri dishes with agar containing [^{14}C]sucrose. Dishes with the excised tips were exposed to four light regimes for 48 h, R + FR, R, B, and B + FR, while light of low intensity (7 w m^{-2} by four layers of cheesecloth) and dark controls were included. Light treatments which included both R and FR were most effective in promoting sucrose uptake by the isolated tips (Table V). Blue light was equal to dark control, even when FR was present.

DISCUSSION

The accompanying article (11) shows that darkening young shoots considerably reduced growth and flower bud development and decreased translocation of ^{14}C-labeled assimilates to the shoot and especially to the shoot tip. Here, it has been demonstrated

Table III. *Effect of Monochromatic, Low-energy Light Given to Darkened Shoot Tip on Translocation of ^{14}C-labeled Assimilates.*

Light was applied intermittently by means of optic glass fibers for 48 h.

Light Treatment to Shoot	Irradiance Energy	Plant Number	Shoot Tip[a]		Whole Shoot[a]	
			Methanol-soluble ^{14}C Translocated Out of Source	RSA	Methanol-soluble ^{14}C Translocated Out of Source	RSA
	$w\ m^{-2}$		%		%	
Full light control	45	4	4.9 ± 2.1a	14.5 ± 5.4ab	71.8 ± 17.2a	3.5 ± 0.9ab
Dark control		12	0.5 ± 0.3b	4.4 ± 3.4b	22.3 ± 14.4b	2.7 ± 1.3b
R, 660 nm	2	4	6.7 ± 4.0a	38.2 ± 18.9a	50.4 ± 22.2ab	7.4 ± 2.5a
FR, 728 nm	1.5	5	4.4 ± 2.6a	11.1 ± 4.6b	39.8 ± 2.7b	4.4 ± 1.6b
B, 455 nm	0.3	5	0.9 ± 1.1b	7.9 ± 9.6b	27.9 ± 17.8b	2.6 ± 2.1b

[a] Values are ± SD. Each parameter number with different letters differs significantly at $P = 0.05$ (Duncan's multiple range test).

Table IV. *[^{14}C]Sucrose Uptake in Vitro by Rose Shoot Tips*

Shoot tips were illuminated *in situ* for 48 h by a beam of monochromatic light, after being darkened for 5 days; the rest of the shoot remained darkened. Control shoots were held in full light. Tips then were excised and incubated for 3 h in 5 mM sucrose solution (0.24 mCi/mmol). Data is of two different experiments employing R or FR light, which included dark controls as well as shoots exposed to full light. The values are means of six replicates ± SD.

Light	Light Intensity	Sucrose Equivalent	Dark Control in Each Experiment
	$w\ m^{-2}$	*μmol/g dry wt*	%
Full light	45	11.0 ± 6.2	340[a]
R, 668 nm	2	4.2 ± 0.7	170[a]
FR, 730 nm	1.5	2.4 ± 0.7	81
B, 450 nm + FR	4.8	3.0 ± 0.9	62

[a] Significantly different at 1% from their dark controls (*t* test).

that the perception of the light reaction promoting the sink activity is in the tip itself since localized lighting of the darkened shoot tip by a very narrow light beam of very low irradiant energy greatly promoted accumulation of ^{14}C-labeled assimilates in the tip (Tables III and IV).

Here, we have tried to characterize this light reaction by various types of experiments. Lighting whole plants with mixed Fl and In light increased assimilate translocation to the uppermost young shoot of rose plants in comparison to Fl light alone. This increase in translocation was accompanied by increased growth of this shoot and decreased number of axillary buds sprouting (Tables I and II; Fig. 2), features that characterize the phenomenon of apical dominance (12). It is known that light, rich in FR, increases apical dominance (7, 17, 18). The findings presented here show a clear linkage between increased apical dominance and promotion of mobilizing ability of the apical bud. These results may be interpreted in two ways: (*a*) incandescent light promoted a factor involved in inhibition of axillary buds, and the increased translocation to the uppermost shoot stemmed from the reduced competition on the available assimilates; (*b*) the increased inhibition of axillary buds stemmed from the light-promoted sink activity of the uppermost shoot. Our results support hypothesis *b* since light did not decrease growth (Table I) and translocation (Table II) to the second shoot.

There seems to be only two studies on the effect of colored light on translocation or absorption of assimilates. Hartt (4) found promotion of basipetal translocation in detached sugar cane leaves by R and B. In her study, FR was as ineffective as the dark treatment. However, Hartt's model did not include a growing sink since only the translocation within the leaf was measured. The importance of a sink to the translocation process is well-established (10, 11, 14, 20). In the first experiment here (Table I), the whole plant was exposed to the light of different spectra. The results obtained were a function of the combined effects on the source leaves and on the competing sinks. In further experiments, the authors studied the direct effect on light of different spectra on the sink itself, as was manifested by translocation of ^{14}C-labeled assimilates to the lighted shoot tips and by testing the ability of detached shoot tips to absorb [^{14}C]sucrose *in vitro*. This was done either by lighting the shoot tip *in situ* by means of optic glass fibers prior to excision or by exposing the detached tips to light of different spectra composition. These techniques were used since absorption of sugars *in vitro* is considered to express the sink strength (1, 3, 20). Of the monochromatic, low-energy light tested here (R, FR, and B), R was the most effective in increasing the transport of ^{14}C-labeled assimilates to the intact tips (Table III) and the uptake of [^{14}C]sucrose by detached ones (Table IV). FR had little effect or no effect in this reaction and B was not active. The effect of F and FR on the uptake of [^{14}C]sucrose *in vitro* are in line with those of Goren and Galston (2) with detached pea epicotyls. It was found, however, that, when FR was added to R, it greatly increased the R-promoted effect (Fig. 3; Table V). FR, when added to B, was ineffective as B given alone (Table V). This may explain the promotive effect of mixed Fl and In light over Fl alone on assimilate transport to the apical bud (Table II). A requirement of mixed R and FR for optimal response is known for some phytochrome reactions, like those promoting flowering in many long-day plants (19). In the experiment in which FR was added to the R (Fig. 3; Table V), not only the spectral composition of the light source was changed, but its total energy was doubled. This may have also accounted for the promotive effect of the added FR. However, it is known that morphogenetic response in plants is proportional to the logarithm of light intensity (15). This is well-demonstrated by results presented in Table IV, where light energy in full light was 22 times higher than in R, but sucrose uptake was only slightly more than 2-fold higher. Therefore, the great promotion of the R effect by FR cannot be due to the added light energy only. Promotion or enhancement of photomorphogenetic events by FR is not yet fully understood. Recently Porath *et al.* (13) suggested that R and FR light action in plants is through different perception sites. In cucumber seedlings, the R perceptive site was shown to be localized in the hook whereas the perception of FR was disperse (13).

The effect of light on sink activity is apparently not related to its effect on energy supply since no differences in ATP level were found between darkened and lighted tips (11). Light, however,

Table V. *[^{14}C]Sucrose Uptake in Vitro by Rose Shoot Tips Illuminated by Colored Light during 48-h Incubation Period*

The tips were harvested 14 days after sprouting of shoots and planted on agar containing 3% sucrose (7.8 μCi/mmol) in Petri dishes under beakers covered with light filters. The incubation was carried out in growth cabinets illuminated by Fl or mixed Fl and In light. The values are means of five replicates ± SD.

Light in Growth Chamber	Filter	Light Energy in Different Spectrum Range			Sucrose Equivalent	Dark Control
		B	R	FR		
		μw cm^{-2} nm^{-1}			*μmol/g fresh wt·48 h*	*%*
Fl (25 w m^{-2}) + In (30 w m^{-2})	Aluminum foil				13 ± 3	100
	B (celluloid 1460)	1.1		2.7	15 ± 4	119
	White (4 layers)	0.6	1	1	23 ± 8	175
	R cellulose (4 layers)		3.4	3.2	26 ± 7	205
Fl (50 w m^{-2})	R cellulose (1 layer)		3		17 ± 4	128
	B (celluloid 1460)	1			15 ± 5	116

may affect the unloading process in the tip by influencing the membrane transport similarly to its promotive effect on ion transport (5).

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