

Communication

Light-Regulated Gravitropism in Seedling Roots of Maize¹

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ABSTRACT

Red light-induced changes in the gravitropism of roots of *Zea mays* variety Merit is a very low fluence response with a threshold of 10^{-9} moles per square meter and is not reversible by far red light. Blue light also affects root gravitropism but the sensitivity of roots to blue is 50 to 100 times less than to an equal fluence of red. In *Z. mays* Merit we conclude that phytochrome is the sole pigment associated with light-induced changes in root gravitropism.

In many cultivars of maize if caryopses are germinated in darkness the primary roots are plagiotropic (*i.e.* grow parallel or nearly parallel to the surface) (1, 3, 6, 8). Illuminating these roots induces gravitropic curving, with R² (660–670 nm) and to a lesser degree B (410–640 nm) particularly effective in promoting downward curving (1, 3, 5–9). However, disagreement exists as to whether this response is controlled exclusively by phytochrome or whether another distinct B light-absorbing pigment is involved. Suzuki and Fujii (8) were unable to reverse the promotive effects of R with a subsequent FR (730 nm) light treatment and therefore concluded that the gravitropic response in *Zea* roots “may not be controlled by phytochrome.” On the other hand, Shen-Miller (7) and later Mandoli *et al.* (3) were able to prevent R-induced curving by following the R with FR. These workers concluded that light-induced gravitropism in maize roots was mediated by phytochrome. In this investigation we have re-examined the issue of phytochrome control of root gravitropism. We provide data which suggests that the VLF of phytochrome (2) is an equally plausible explanation for the inability of some workers to obtain FR reversibility. In addition, we have investigated whether the reported effects of B on root curving could be associated with a pigment different from phytochrome.

MATERIALS AND METHODS

Materials. *Zea mays* cv. Merit (obtained from Asgrow Seed Co., Tracy, CA) was used for this work. Caryopses were imbibed for 2 h in the dark in rapidly running warm water (25°C). Following imbibition caryopses were distributed into trays (35 × 20 × 4 cm³) lined with paper towels moistened with distilled H₂O. Trays were sealed with aluminum foil and placed in a 23

to 25°C dark room. Forty-two to forty-eight h later in very dim green light (1×10^{-10} mol m⁻² s⁻¹; from a Nikon 6 V, 30 W tungsten bulb filtered through three layers of Rohm and Haas green plastic [2092]) seedlings with straight roots 15 to 30 mm in length were selected. Each seedling was exposed to this light for no more than 10 s.

Experimental Protocol. A pin was inserted through individual

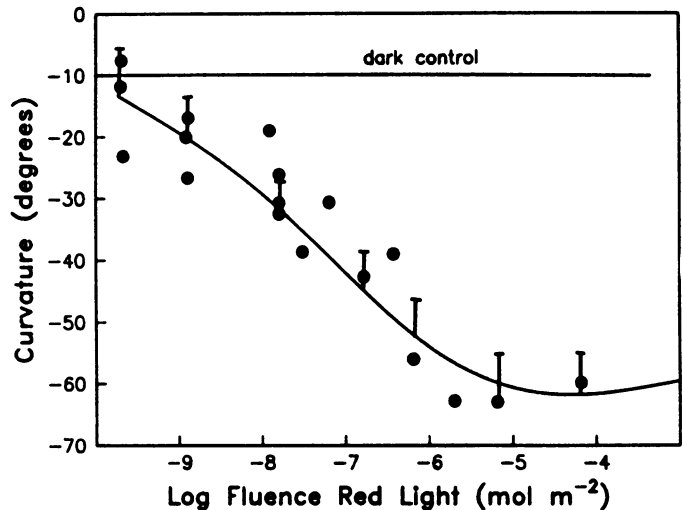


FIG. 1. R fluence response curve of maize roots, cultivar Merit. Fluence rate was varied with Balzers neutral density filters.

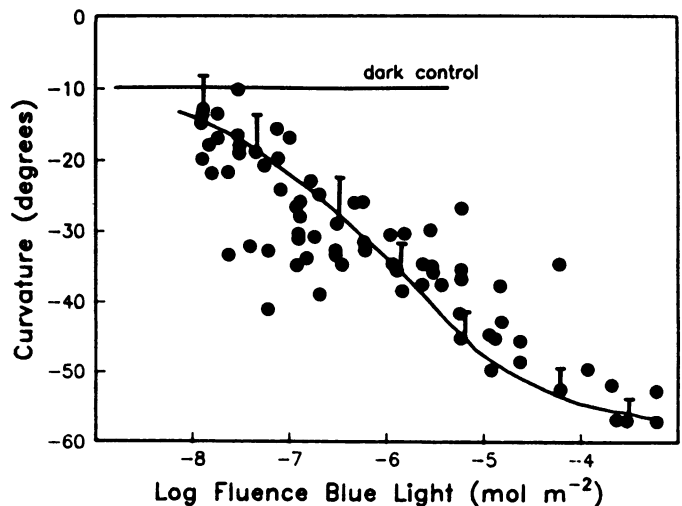


FIG. 2. B fluence response curve of maize roots, cultivar Merit. Fluence rate was varied with Balzers neutral density filters.

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² Abbreviations: R, red light; B, blue light; FR, far-red light; VLF, very low fluence.

Table I. Curvature of Roots of *Z. mays* Cultivar Merit Exposed to a Sequence of R or FR Light

Caryopses were irradiated 42 to 48 h after imbibing. The FR immediately followed the R. At least 40 roots were used for each treatment.

Light Treatment	Curvature
<i>mol·m⁻²</i>	<i>degrees ± SEM</i>
R (7×10^{-8})	30 ± 3
R (7×10^{-8}) + FR (4.4×10^{-5})	54 ± 4
FR (4.4×10^{-5})	43 ± 3
FR (4.4×10^{-4})	44 ± 2
R (1.7×10^{-5})	57 ± 5
R (1.7×10^{-5}) + FR (6×10^{-3})	40 ± 4
R (1.7×10^{-5}) + FR (1.2×10^{-2})	43 ± 3
FR (6×10^{-3})	40 ± 3
FR (1.2×10^{-2})	38 ± 5

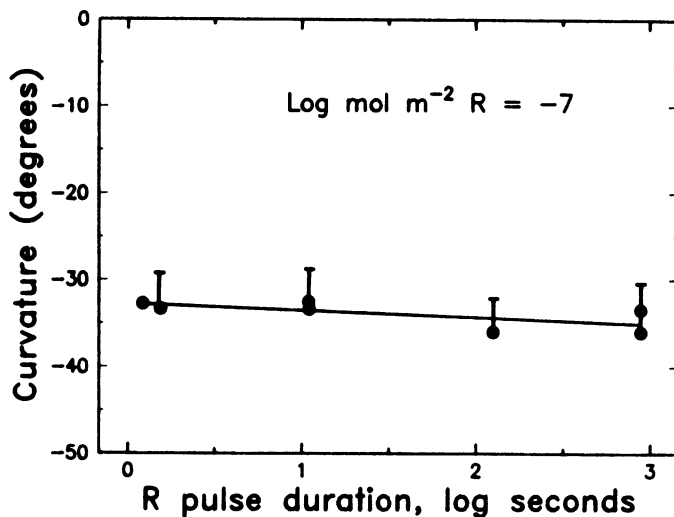


FIG. 3. Reciprocity characteristics of R-irradiated maize (Merit) roots. Fluence rate was varied with Balzers neutral density filters. Duration of exposure was varied from 1 to 1000 s. Fluence was held constant at $10^{-7} \text{ mol} \cdot \text{m}^{-2}$.

kernels and the root oriented horizontally by pinning it to a styrofoam board covered with moistened paper towels. Roots were irradiated perpendicular to the future direction of curving and then placed in moist (RH 95%), light-tight chambers. Three to five h later the degree of gravitropic curving was recorded by making xerox copies of the roots. Each data point in the accompanying figures represents the response of at least 8 to 10 roots, \pm SEM.

R and FR light were obtained using broad band filters according to Mandoli and Briggs (2). Blue light was obtained using a Corning blue glass filter No. 5-60, peak 435 nm. The quantum flux densities were altered by passing light through neutral density filters (Balzers, ND-1x, -2x, -4x).

RESULTS

Light Fluence and Gravitropic Responsiveness in *Z. mays*, Variety Merit. Red light induces downward curving in roots of Merit with maximum curvature attained 3 to 3.5 h after irradiation. The threshold for the response was difficult to determine precisely but is at a fluence of approximately $10^{-9} \text{ mol} \cdot \text{m}^{-2}$ R. The response saturates at a fluence of 10^{-5} to $10^{-6} \text{ mol} \cdot \text{m}^{-2}$ R, with roots showing a maximum curvature of approximately 60° (Fig. 1). Dark control roots (exposed briefly to green light, approximately $5 \times 10^{-10} \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) show a curvature of about 10° . Blue irradiation also induced curvature with a threshold of

about $10^{-7} \text{ mol} \cdot \text{m}^{-2}$ (Fig. 2). The response saturates near $10^{-4} \text{ mol} \cdot \text{m}^{-2}$, again with a final curvature of nearly 60° .

The promotive effects of a saturating fluence ($1.7 \times 10^{-5} \text{ mol} \cdot \text{m}^{-2}$) of R light on curving could only be reversed partially by FR. Indeed, FR alone ($4.4 \times 10^{-5} \text{ mol} \cdot \text{m}^{-2}$) promoted significant curvature (Table I). A subsaturating fluence of R ($2 \times 10^{-7} \text{ mol} \cdot \text{m}^{-2}$) will produce the same magnitude of curvature whether given over 1, 10, or 1000 s (Fig. 3). Hence the reciprocity law is valid over this range.

DISCUSSION

Light-induced gravitropic curving in roots of *Z. mays* variety Merit is mediated exclusively by phytochrome and does not involve a separate B light absorbing pigment. Blue irradiation is effective at inducing root curving, but the fluence of B required for induction was well as for maximum curvature (60°) is 50 to 100 times greater than the fluence of R needed for these same responses (Figs. 1 and 2), and is near the ratio for phytochrome phototransformation by B and R *in vivo* in maize coleoptiles (4). Thus our interpretation is that in Merit, B is effective via phytochrome phototransformation.

Shen-Miller (7) reported that in the maize variety Wisconsin hybrid 64A \times 22 R, B light was effective in inducing root gravitropism and that the promotive effects of B could be reversed by FR light. Her data thus also argue against the participation in gravicurvature of a separate B light absorbing pigment distinct from phytochrome. In cress, however, Hart and MacDonald (1) argue that the gravicurvature differs between R- and B-irradiated roots. Using equal fluences of R and B, these workers report a curvature of $49 \pm 2^\circ$ for R-irradiated roots and a curvature of $54 \pm 3^\circ$ for B-irradiated roots. Because of this supposed difference in the degree of curvature, these workers have argued for the participation of a B light absorber distinct from phytochrome, in light-induced root curving in cress. However, since fluence response curves were not provided for either R or B, we do not know the threshold fluence for curvature induction, nor the fluence at which maximum gravicurvature (saturation) was attained. Knowing such information is important for determining the relationship of a particular fluence to the gravicurvature response. For example, if the fluence of B used was great enough to saturate the phytochrome response (via the absorption of phytochrome in the B) one would not expect to see any significant statistical differences in the maximum angle of curvature between R- and B-irradiated roots. Thus, we would suggest that for cress fluence response curves for both B and R are required before one can make any definitive statement as to whether phytochrome alone or phytochrome and separate B light photoreceptors play a role in light-induced gravicurvature.

In *Z. mays* Merit the inability of FR light to reverse completely the promotive effects of R would by itself argue against a role for phytochrome in root curvature. This observation however, coupled with the high sensitivity of roots of *Z. mays* Merit to R (threshold $10^{-9} \text{ mol} \cdot \text{m}^{-2}$) classify this response as a phytochrome-mediated very low fluence response (VLF) (see Mandoli and Briggs [2]). As reported for other cultivars of maize (3), in Merit also, fluence and pulse duration can be varied reciprocally over long periods of time (1–1000 s) without failure of reciprocity (Fig. 3). Thus in roots showing a VLF response reciprocity still holds.

Suzuki *et al.* (8, 9) working with maize (variety Golden Cross Bantam 70) and Hart and MacDonald (1) working with cress were unable to reverse the effects of R with FR light. These workers therefore concluded that phytochrome was not likely associated with light-induced root curving. However since equal fluences of both R and FR were used it is not too surprising that photoreversal was not observed. For as Mandoli *et al.* (3) have shown, complete photoreversibility of light-induced root gravi-

tropism can require that the FR fluence be at least 100 times greater than the R. This is also the case with R-light induced inhibition of mesocotyl elongation (10). Here too FR must be 100 to 1000 times greater fluence than the R in order to bring about photoreversibility. Thus, if one is to exclude a role for phytochrome based solely on a lack of FR reversibility, it is necessary to have fluence response curves for both R and FR, and also to show that the FR alone is ineffective.

From our work and an analysis of the literature we conclude that phytochrome is the only pigment mediating light-induced gravitropic bending in roots.

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