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Light gradients in shoots subjected to unilateral illumination—implications for phototropism

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Abstract. When an organ is subject to unilateral illumination, light entering the organ is attenuated very efficiently and the irradiance at the 'shaded' surface is only a small percentage of that at the illuminated surface. The light gradient across the organ is approximately exponential, being steepest across the first few cell layers. The penetration of light into an organ was found to be similar with red or blue light and was largely independent of the pigmentation of the organ. Studies of light transmission in organs infiltrated with liquids of different refractive index showed that refraction and reflection were the main factors in establishing the light gradient in organs.

The implications of the measured light gradients are discussed briefly in relation to models of phototropism.

Key-words: phototropism; light gradients; scattering; optical properties.

Introduction

The study of phototropism is complicated by the fact that any treatment giving rise to the response does so by applying a differential stimulus across the radial axis of the responsive organ. The light flux incident on the cells at the illuminated surface can easily be measured. However, the light doses received by internal cells or by the peripheral cells on the shaded side of a unilaterally illuminated organ are less easily measured. The importance of a light gradient to the phototropic response has been appreciated for many years but surprisingly few attempts have been made to quantify it or to establish which of the optical properties of the organ are responsible for its generation.

Blaauw (1915) attempted to measure such light gradients using a photographic technique and reported that up to 25% of the incident light striking a unilaterally illuminated hypocotyl reached the shaded side. He proposed that this light gradient caused a gradient of growth inhibition across the organ, thus producing curvature. However, a later study of coleoptiles, conducted by Dillewijn (1927), reported that only 3% of the incident light was transmitted to the shaded side. These values for the transmission of light do not, however, provide a full and adequate description of the gradient since they merely describe the extremes. The light dose received by each cell, at all positions in the responding organ must eventually be determined; only then will it be possible to relate the response of each cell to the magnitude of the stimulus it receives. The present investigation reports a more detailed study of the light gradients in unilaterally illuminated organs and discusses the optical properties of these organs in relation to the measured gradients.

Materials and Methods

Plant material

Sunflower and Broad Bean. Seeds of sunflower *Helianthus annuus* (Hybrid 891, generously donated by Interstate Seeds, North Dakota) and the broad bean, *Vicia faba* (var. Aquadulce Claudia) were soaked in running water for 3 h prior to sowing in wet vermiculite. Seedlings were germinated and grown in darkness at 25 °C and 80% humidity for 5 d when plants of 4–5 cm in length were obtained. In experiments where de-etiolated plants were required, seedlings were subsequently exposed to white fluorescent lighting (40 μmol m^{-2} s^{-1}) at 25 °C for 30 h.

Oat. Seeds of *Avena sativa* (var. Victory) were freed from their husks (glumes) and soaked in running water for 3 h. The seeds were then laid embryo uppermost on saturated blotting paper after the method of Went & Thimann (1937). Following 24 h germination in the dark the seeds were exposed to 3 h red light (40 μmol m^{-2} s^{-1}), to suppress mesocotyl growth and to produce straight coleoptiles (Lange, 1927; du Buy & Nuernbergk, 1929). Plants were then grown in darkness in wet vermiculite at 25 °C and 80% humidity for 4 d until plants reached a usable length (25 mm).

Light sources

Red light, which suppressed mesocotyl growth, was obtained by filtering light from an Atlas De Luxe Natural Fluorescent tube through one layer of No. 1 (yellow) and one layer of No. 14 (ruby) Cinemoid (Rank Strand, Brentford, U.K.) filter (Smith, 1975). The dim green safelights (0.1 nmol m^{-2} s^{-1}) used for

all pre-experimental manipulations and watering were constructed using three layers of No. 39 (green) Cinemoid covering a Philips 20 W Natural Daylight fluorescent tube.

Blue light (5 nmol m^{-2} s^{-1}) was obtained using a custom built fibre optic light source. Light from a 100 W projector bulb (Philips 7724) was passed through a narrow band interference filter (460 ± 20 nm, Edmunds Scientific, Barrington, NJ, U.S.A.) and emerged through a narrow slit (0.2 mm) at the end of a flexible fibre optic light guide (Barr and Stroud, LE5/3.5/1000).

Monochromatic red light (632.8 nm) was obtained using a Spectra-Physics model 155A Helium-Neon laser (0.4–0.7 mW output).

Light measurements

Light measurements were made using a Macam photometer (PR 3010, Macam Photometrics, Livingston, Stirling, Scotland) fitted with a photodiode (Macam PD 102) for red measurements or with a photomultiplier (Macam PM 103) for blue measurements. When measuring axial transmission, the geometry of the Macam detectors was unsuitable, hence a 1 mm^2 PIN photodiode (RS Components, London, type 305–462), coupled via a J-F.E.T. amplifier (RS Components, type 355) to a 3.5-digit digital voltmeter, was used.

A light beam was directed at either the whole organ or a section of the organ. Thin sections were obtained by peeling off the peripheral cell layers. The tissue was then mounted over a small slit aperture on a piece of black card. The light emergent from the tissue, along the same axis as the incident beam, was measured using a short fibre optic light guide (acceptance angle 60°) attached to either the Macam photodiode or photomultiplier. In such studies (Figs 2–4 and 10), the incident beam was always orthogonal to the curved surface of the tissue section (Fig. 1).

Inhibition of carotenoid synthesis

Seeds of sunflower and oat were grown as above except that, after 3 h imbibition, the seeds were soaked for an additional 48 h on filter paper saturated with 0.1 mol m^{-3} SAN 6706 (Sandoz-Wander Inc., Homestead, Florida, U.S.A.). Oat coleoptiles were grown on the filter paper whereas the sunflower seeds were transplanted to vermiculite. This concentration of Sandoz was found to inhibit carotenoid accumulation by 90–95%.

Dehydration and vacuum infiltration

Sunflower hypocotyls were infiltrated with water (refractive index 1.33) or with cedarwood oil (refractive index 1.52). When infiltrating with water, the hypocotyls were placed in a Buchner flask with water and the flask sealed. A vacuum of one atmosphere was then applied and the flask kept at 0 °C to minimize the risk of damage to the tissues during infiltration. The percentage transmission through these tissues was measured after 48 h of infiltration.

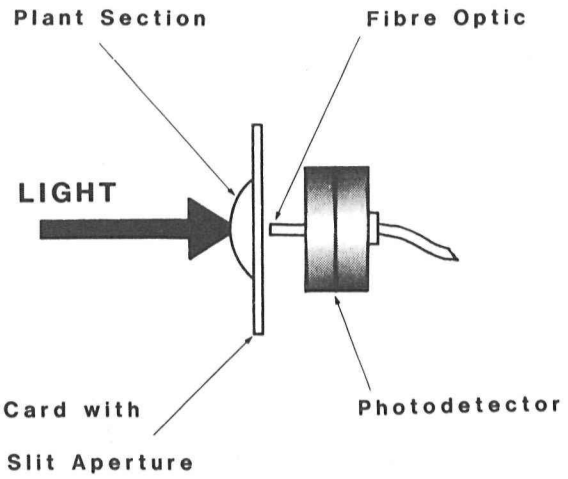

Figure 1. Diagrammatic representation of the arrangement of the light source, plant organ and light detector used to obtain the data in Figs 2–4 and 10.

As cedarwood oil is water immiscible, the hypocotyl sections were dehydrated prior to infiltration, using the method of O'Brien & McCully (1981). In the first four solutions in this sequence polyvinyl polypyrrolidone was added in an attempt to reduce browning due to the oxidation of phenolic compounds. The hypocotyl segments were sectioned prior to dehydration and infiltration, as it was found difficult to do so afterwards. Infiltration also had to be a gradual process to minimize tissue damage so the following ethanol–cedarwood oil sequence was used: 5, 10, 15, 20, 30, 40, 60, 75, 85, 100% cedarwood oil. The vacuum was again 1 atm and the temperature was kept at or below 0 °C for 3 d whilst the infiltration sequence was completed.

Axial transmission of light

The percentage axial transmission of light was investigated in two ways. Firstly, longitudinal hypocotyl sections of decreasing length were introduced into a laser beam (Fig. 11, Beam A) and the percentage axial light transmission measured. In the second method longitudinal hypocotyl sections were passed through a light beam orthogonal to their long axis (Fig. 11, Beam B). Light being transmitted axially was measured by placing a photodiode at the base of the hypocotyl section (see Fig. 11) in the manner reported by Mandoli & Briggs (1982a) and Mandoli & Briggs (1982b).

Ray tracing studies

A photomicrograph of a transverse section of a sunflower hypocotyl was kindly supplied by Dr

C. S. M. Carrington (Carrington, 1982). The image of a small part of the section showing the five outermost cell layers was enlarged to final dimensions of 1.05×0.90 m by tracing the projected image onto paper. The hypocotyl was assumed to consist of four homogeneous and isotropic optical media namely: air, cuticle, cell wall and cell sap. Because the dimensions, distribution and refractive indices of mitochondria, nuclei, chloroplasts and other cell organelles is largely inknown, the optical effects of these structures was ignored, although they undoubtedly produce some scattering. The refractive indices of the four media considered were taken to be; air = 1.00, cell wall = 1.52 (Renck, 1972), cell sap = 1.36 (Charney & Brackett, 1961) and cuticle = 1.45 (Weat, 1976) considered to be equivalent to the cuticle of the cape berry (*Myrica cardifolia*).

Using the approach of Kumar & Silva (1973) the fate of incident light rays was followed. Geometrical optics were assumed to be valid for the media of the hypocotyls mentioned above and using Snell's Law, Fresnel's equations and geometrical construction the paths of random incident rays at both oblique and normal angles of incidence was followed.

Results

A beam of red light from a laser was directed orthogonally to the curved surface of an etiolated hypocotyl and the irradiance along this same axis was measured for different thicknesses of tissue (Fig. 2a). It was apparent that irradiance declined rapidly, a large non-linear light gradient being established. The attenuation was greatest over the first few cell layers and the average irradiance 0.5 mm into the hypocotyl was only 10% of that striking the illuminated surface. The irradiance at the shaded side of the organ, directly opposite the point of incidence of the light was less than 2% of that at the illuminated surface. If a semi-log plot of optical density or absorbance versus section thickness is drawn (Fig. 2b) it is evident that the data points do not lie on a single straight line, two straight lines intersecting at a point corresponding to a section thickness of approximately 0.8 mm giving a better fit. This feature also shows up if the data from Figs 3 and 4 are drawn as semi-log plots.

Repeating these measurements with blue light also produced identical results for dicotyledons (Fig. 2a) and similar data were obtained for coleoptiles (Fig. 3). This wavelength independence suggests that light absorption was not of fundamental importance in generating the gradient. Support for this conclusion came from comparisons of light gradients in plants with altered pigmentation. De-etiolated hypocotyls with higher concentrations of pigments (Fig. 2) and coleoptiles (Fig. 3) and hypocotyls (Fig. 4) with reduced carotenoid levels all showed similar light gradients to etiolated organs.

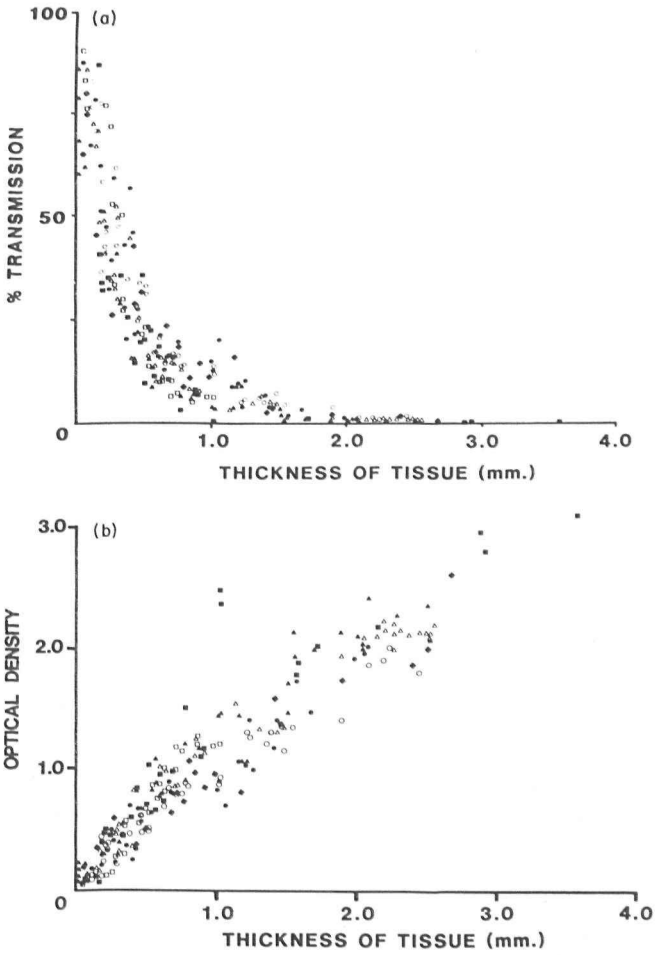

Figure 2. (a) The radial transmission of light through the hypocotyls of the sunflower (*H. annuus*) and broad bean (*V. faba*) as a function of tissue thickness. (b) Semi-log plot of the data from Fig. 2a plotted as optical density (absorbance) *v.* thickness of tissue. Symbols as for Fig. 2a. □. *Vicia:* etiolated, red light; ■, *Vixia:* de-etiolated, red light; ◆, *Vicia:* etiolated, blue light; △, *Helianthus:* etiolated, red light; ▲, *Helianthus:* de-etiolated, red light; ○, *Helianthus:* etiolated, blue light; ●, *Helianthus:* de-etiolated, blue light.

Our attention turned to 'light scattering'* after it was observed that when a piece of the peripheral cell layers peeled from a hypocotyl was interposed in the laser beam, the beam was diffused very effectively (Fig. 5). Obviously the light passing through this piece of tissue, only two or three cells thick, was being refracted and reflected causing the light to be dispersed. Many interfaces exist between media of different refractive indices and since light strikes these interfaces at a variety of angles, numerous opportunities for refraction and reflection occur (Figs 6 and 7). This can be demonstrated diagrammatically in two dimensions by using the ray tracing method of Kumar & Silva (1973).

*It should be recognized that the term 'scatter' used in this context simply describes the diffusion of light by refraction and reflection and not scattering in the exact physical sense (i.e. Rayleigh scattering).

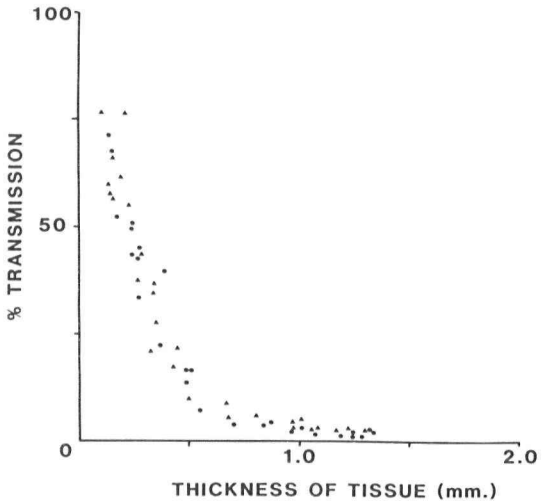

Figure 3. The radial transmission of blue light through etiolated coleoptiles of oat (*A. sativa*) as a function of tissue thickness. ●, Control; ▲, treated with Sandoz to inhibit carotenoid synthesis.

The paths for a random selection of rays incident at normal angles to the surface are shown in Fig. 6 and it is evident that many such rays would be deflected very significantly from their initial direction within a few cell diameters from the surface. Considering the case for rays incident at more oblique angles (Fig. 7), it is clear that more dramatic deviations from the initial direction occur.

The reflected and transmitted light intensities for ray X (Fig. 6), a normal incident ray which hardly deviates from its path after entry and ray Y (Fig. 7), an obliquely incident ray which deviates a great deal after entry, are shown in Figs 8 and 9, respectively. For ray Y, at any interface at which the reflected ray was $>10\%$ of the incident ray, the path of the reflected ray was also plotted.

Further support for the role of refraction and reflection in generating the light gradient came from

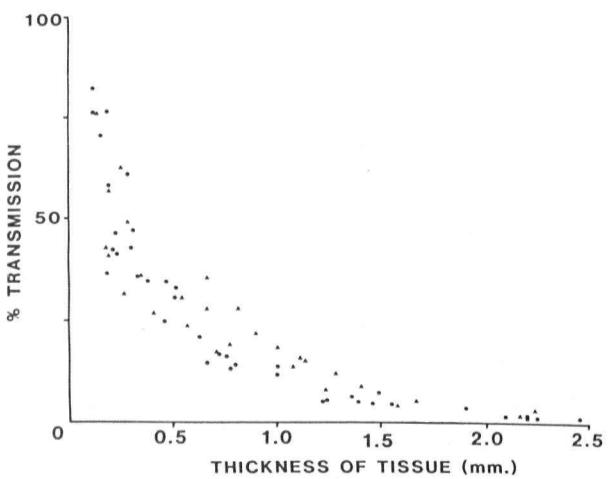

Figure 4. The radial transmission of blue light through etiolated hypocotyls of sunflower (*H. annuus*) as a function of tissue thickness. ●, Control; ▲, treated with Sandoz to inhibit carotenoid synthesis.

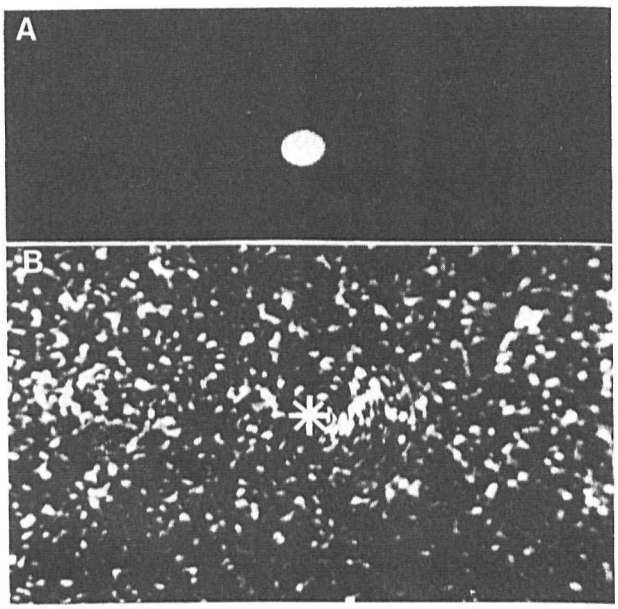

Figure 5. (a) The image of a coherent beam of light from a laser. (b) The image of the same beam with an epidermal peel (two or three cell layers thick) from an etiolated sunflower hypocotyl placed in the beam. The ✱ marks the position of the centre of the beam.

studies of light transmission through hypocotyl sections infiltrated with media of different refractive indices. Vacuum infiltration of the air spaces with water increased the penetration of light into the hypocotyl (Fig. 10) suggesting that the intercellular air spaces play a significant role in the creation of the light gradient. However, when a section was completely infiltrated with cedarwood oil, effectively creating a medium of homogeneous refractive index (approaching that of the cell walls), the section became nearly transparent and light transmission increased dramatically (Fig. 10).

When the light transmission experiments were repeated with the organ oriented axially to the light beam, light was found to penetrate much more efficiently into the organ than when the light was incident radially (Fig. 11). This can be partially explained when one examines a longitudinal section of a sunflower hypocotyl. The cells are elongated and it is evident that the number and angle of the interfaces between media of differing refractive indices is such that less refraction and reflection would be expected. However, if the longitudinal transmission is measured when the beam is directed radially, the transmission was, as expected, very low (Fig. 11).

Discussion

The data presented show that very large gradients of light can be generated across unilaterally illuminated plants. The observed gradients, which can exceed 50 : 1 between the illuminated and shaded sides, are much greater than the 4 : 1 ratio reported by Blaauw

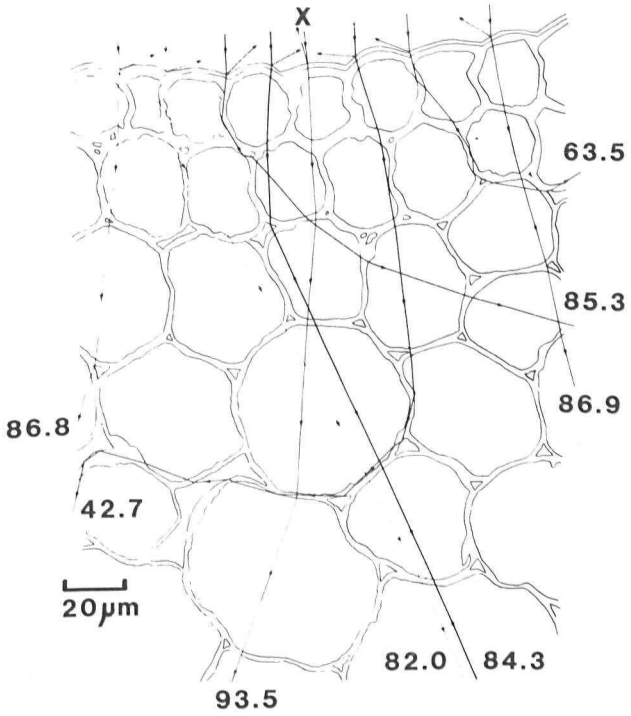

Figure 6. A cross-section of the outer 5 cell layers of an etiolated hypocotyl of a sunflower (*H. annuus*). The pathway of seven rays normal to the surface are shown together with the transmitted intensity at the end of each ray.

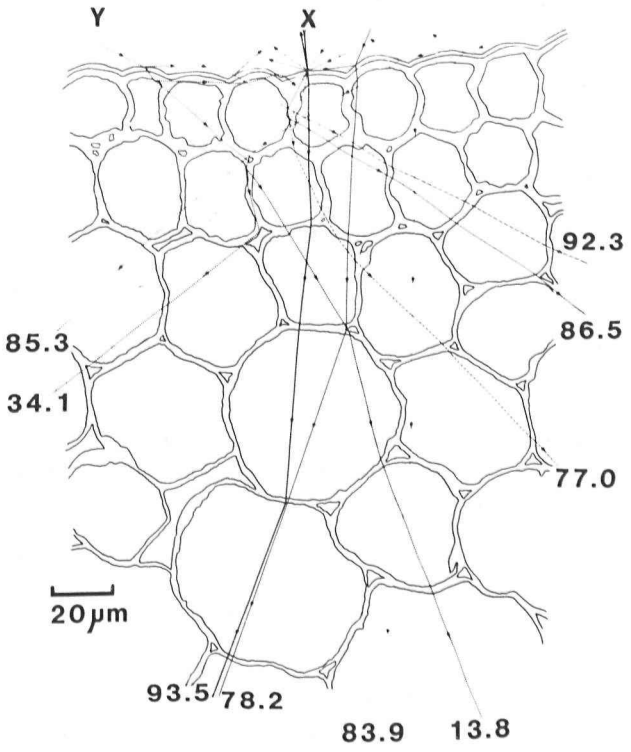

Figure 7. The same cross-section as in Fig. 6. The paths of rays incident at oblique angles being followed. The transmission again being indicated at the end of each ray.

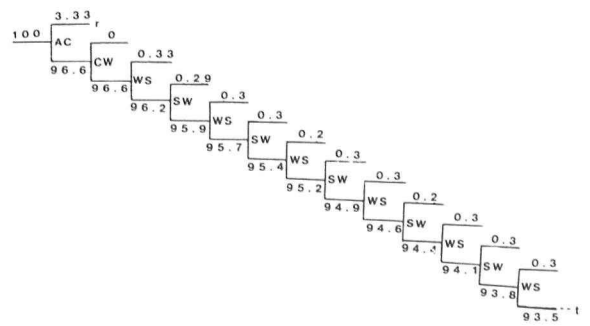

Figure 8. A diagram indicating the fate of the light energy for ray X in Fig. 6 as it passes through the section, the ray having an initial arbitrary value of 100. A = air, C = cuticle, W = cell wall, S = cell sap, hence WS = light passing from cell wall to cell sap; r = reflected ray; t = transmitted ray; T = total internal reflection of ray.

(1915) but it must be noted that he used a photographic method of measuring light which was more difficult to quantify. Our measurements are, however, in good agreement with those of van Dillewijn (1927) for *Avena* coleoptiles and are similar to the gradients of UV light in coleoptiles calculated by Wang, Hamilton & Deering (1968).

The methods used in the present study obviously cannot provide a measurement of the light flux through any point in a shoot because the measuring devices were directional and could only detect light leaving the cells adjacent to the detector at specific angles. Furthermore, when tissue slices were used for measurements, backscatter from the removed cells would of course be absent. The problems associated with the methods used and with alternative methods have been discussed recently by Seyfried & Fukshansky (1983) and by Seyfried & Schäfer (1983). However, the simple methods employed in this study give a qualitative estimate of the light gradients and it seems likely that the magnitude of the real gradients would be underestimated by the failure to measure backscattered light. For instance, the very considerable scatter produced by the outer cell layers (Fig. 5) would increase the flux at points within those layers to a value exceeding the incident flux entering that part of the shoot (Seyfried & Fukshansky, 1983).

Our studies of the possible factors responsible for generating the large light gradients would seem to rule out a significant role for light absorption. It is maybe not surprising, however, that a role for absorption was accepted somewhat uncritically for many years. Ever since Sachs (1865) showed that blue light was the most effective wavelength in causing phototropism, there was uncertainty as to whether this wavelength dependence was a consequence only of the photoreceptor absorption spectrum or whether the dependence was also a consequence of the absorption properties of 'screening pigments' (Bunning, Dorn, Schneiderhorn & Thorning, 1953; Thimann & Currey, 1960). The most recent studies to address the question were

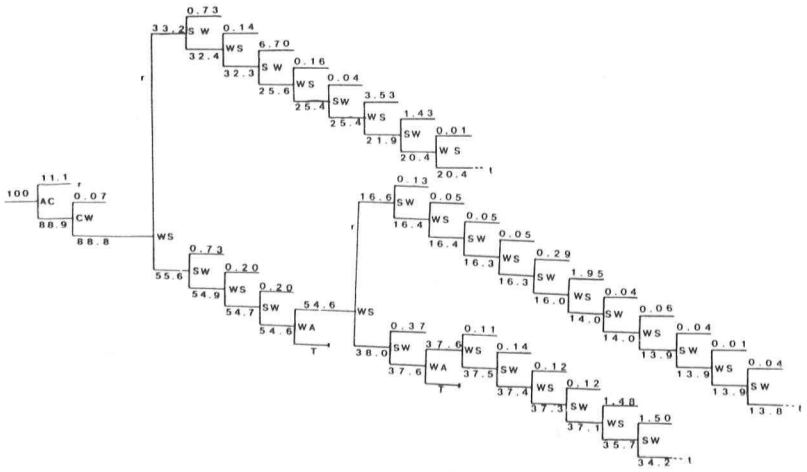

Figure 9. A diagram as in Fig. 8 but following ray Y, abbreviations as in Fig. 8.

conducted on coleoptiles treated with a herbicide which inhibits carotenoid synthesis (Vierstra & Poff, 1982; Poff, 1983). In these studies it was noted that coleoptiles in which carotenoid accumulation had been reduced by 98% still showed 60% of the normal phototropic response and a herbicide effect independent of its effect on carotenoid synthesis was not excluded. These workers recognized that light scattering must contribute to the generation of the light gradient although they regarded it as less significant than absorption by screening carotenoids. The data of Gates, Keegan, Schlecter & Wiedner (1965) and Fukshansky (1981) which showed that plant tissues transmit very little light and, more importantly, that transmission is relatively independent of wavelength is supported by the results from the present study (Fig. 2). In addition, the fact that light is transmitted to a similar extent in etiolated and green shoots (Fig. 2) or in organs with greatly reduced carotenoid levels (Figs 3 and 4) lends further support to the argument that light scattering is the major factor responsible for producing the observed light gradient.

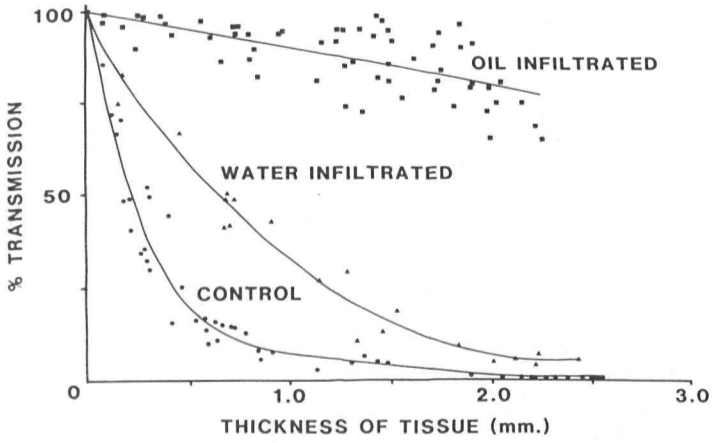

Figure 10. The effect of water infiltration (▲) and infiltration with cedarwood oil (■) on the radial transmission of red light through sections of etiolated sunflower hypocotyls expressed as a function of tissue thickness. The lines shown are least squares fitted polynomial curves for the data.

The light scattering properties of plant tissues have been known to microscopists for many decades but this optical property has been studied rather little by physiologists, except in the case of leaves. As yet there are no satisfactory optical models to describe light propagation in plant tissues. An attempt to use the Kubelka–Munk theory (Kubelka, 1948) to calculate the fluence rate gradient in leaves was made by Holmes & Fukshansky (1979) and Fukshansky (1981). However, it was recognized that the range of validity of the K–M theory precluded its use in this case because implicit in its derivation was the assumption that the screen was infinitely wide such that edge effects may be ignored. Whilst the K–M theory has been further extended to account for fluorescence (Fukshansky & Kazarinova, 1980), the authors state '. . . it is already clear that macro-homogeneous objects provide substantial and perhaps sometimes insuperable obstacles in solving problems (of scattering, screening and fluorescence)'. However, recently a modified K–M approach was used to calculate the light gradients within organs (Seyfried & Fukshansky, 1983) and interestingly it predicted near exponential gradients.

Whilst no adequate quantitative model exists to describe the light gradient in plant tissues, the ray tracing method serves to illustrate how light gradients may be generated. However, in common with all other models it makes certain assumptions. Firstly, it ignores any contribution to the gradient due to absorption, Rayleigh scatter, changes in state of polarization and other physical processes as mentioned by Fukshansky (1981). Secondly, it assumes optical homogeneity and isotropy of the media considered. These assumptions result in a 'worst case analysis' with the transmitted intensities, therefore, being over-estimated. Despite this under-estimate of the light gradient, the method does show how rapidly attenuation can occur (Figs 7 and 9).

The light gradients measured pose some interesting

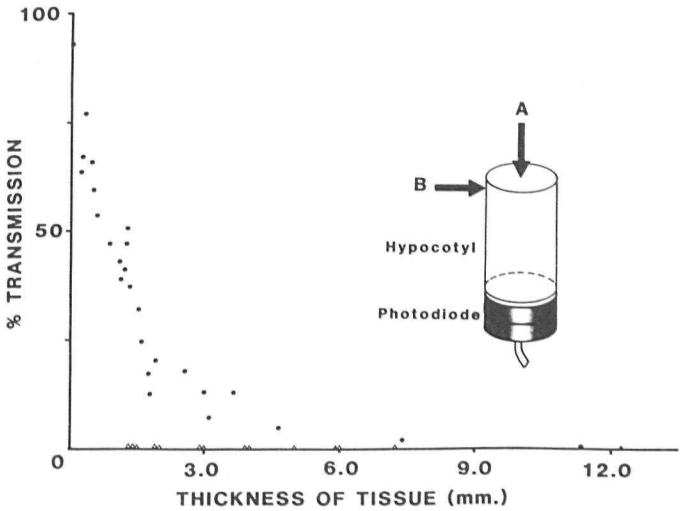

Figure 11. The axial transmission of red light through etiolated hypocotyl tissue of sunflower as a function of axial distance. (a) Light incident axially (●). (b) Light incident radially (△).

problems for those studying phototropism. For instance, at very low irradiance levels used in the first positive curvature experiments, the cells at the shaded side of the organ would not receive a detectable light dose until cells at the illuminated side had received quite a considerable dose. Thus, as the unilateral irradiance levels are increased above the threshold, increasing numbers of cells will be given a detectable dose and can possibly contribute to the response. Any model of phototropism based on a unified organ response (e.g. Cholodny-Went lateral auxin movement model), involving the co-ordinated action of cells across the organ, would presumably demand that the threshold dose for the whole organ might be well above that of the threshold dose for a cell. At all irradiance levels, the light gradient across any cell at the shaded side would certainly be very small compared to the gradient across cells near the illuminated surface. A model of how lateral auxin transport across the organ would occur under the conditions would not seem to be available. The measurements of longitudinal transmission of light in hypocotyls reported in this paper confirm that light penetrates more efficiently along the long axis of cells (Mandoli & Briggs, 1982a, b). However, it seems unlikely that light piping is of general importance because the axial transmission of light in a unilaterally illuminated organ is very low (Fig. 11). Furthermore, if only a small zone of an elongating organ is subject to continuous unilateral blue light, the phototropic response which develops is largely restricted to that zone (Macleod *et al.*, 1984). Further studies are, however, required in coleoptiles where tip illumination may result in considerable transmission of light down the organ (Mandoli & Briggs, 1982a, b) and where there may be better evidence for a transmitted effect following tip illumination, but it seems likely that this is a special case.

In conclusion, it has been shown that light scattering is the prime cause of the light gradient in unilaterally illuminated shoots and that large gradients are established in such organs. Further work is now required to establish the precise nature and location of the relevant photoreceptors in these shoots. Then it may be possible to relate the response of individual cells within the shoot to the light dose that they receive.

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