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Optical properties of etiolated plant tissues

(internal reflectance/light-guiding/acceptance angle/photomorphogenesis/phototropism)

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ABSTRACT **Etiolated tissues of several plants are multiple bundles of fiber optics capable of coherent transfer of light over at least 20 mm. The acceptance angles (the angles at which light can be intercepted and then internally reflected longitudinally) for mung beans, oats, and corn are 47°, 59°, and 52°–54°, respectively. The shapes of the curves that describe the acceptance angles are the same for various tissues of the same plant but differ between species. The pattern of light transmitted longitudinally through a tissue is dependent on the angle at which the light intercepts the side of the tissue and is strongly influenced by the tissue geometry. When 0.5 mm of the tip is irradiated, the amount of light traveling down the "shaded" side of the coleoptile is equal to or 2- to 3-fold greater than the amount traveling down the "lighted" side.**

Internal reflectance of light by etiolated tissues has been discussed cursorily (e.g., refs. 1 and 2) but, to our knowledge, until recently no hard evidence for the phenomenon has been published. The present study was spurred by the discovery of the extreme photosensitivity of etiolated oats: even brief exposure to conventional "safe" light can induce oat photomorphogenesis (3). Even modest light-guiding by the seedlings could allow effective light transmission from the coleoptilar tip to potential sites of photoperception located near the node (4) and thus induce photomorphogenesis well before most of the seedling had emerged from the soil. The logarithm of percentage axial light transmission (at 635 nm) of both oat mesocotyl and leaf tissues is a linear function of tissue length (4). This paper (*i*) shows that axial light transmission is a property of many etiolated plant tissues, (*ii*) details some physical parameters that describe internal reflectance in these organs, and (*iii*) discusses the possible significance of these physical parameters to seedling photobiology.

MATERIALS AND METHODS

Growth of Plants. All seeds were imbibed and all plants were grown in absolute darkness for 2–5 days at 26 ± 1°C. Oat, corn, and mung bean seedlings [*Avena sativa* L., cv Lodi, lot 0170-B, and *Zea mays* L., WF9 × 38, from Dakota Seed and Grain (Watertown, SD); *Phaseolus aureus* L., purchased from a local grocery] were either used immediately or stored at 4°C until used. All manipulations prior to measurement of light-guiding were performed in absolute darkness.

Measurement of Axial Light Transmission by Whole Tissues. Axial light transmission through tissues was quantified by applying light to one end of a deliberately curved tissue segment and measuring the light output at the other end in arbitrary units with a photomultiplier as described (4). However, the light-emitting diode used previously was replaced by a 0.5-mW He-Ne laser (model 155, 0.25 W/cm^2, Spectra-Physics, Mountain View, CA). This laser produces about a 1-mm-diameter monochromatic beam at 632.8 nm. All measurements of axial light transmission were made in dim green light (3). No visible greening occurred in these tissues.

Measurement of the Pattern of Axial Light Transmission Across the Cut End of the Tissue. The patterns of light (or light gradients) across the cut ends of the tissues when narrow beams of laser light were applied to the tissues were sampled by an array of optical fibers (Fig. 1).

RESULTS

Are Etiolated Organs Light-Scattering Cylinders or Optical Wave Guides? Longitudinal light transmission by etiolated tissues (4) could result from simple light scatter through the tissue or could be the result of internal reflection of light within the seedling. The former was not considered likely because (*a*) dim light from a light-emitting diode is axially transmitted over long distances [25–45 mm of etiolated oat mesocotyl (ref. 4; unpublished data)], (*b*) this light is readily transmitted through curved tissues, and (*c*) the sides of the bent tissues that are transmitting light are darker than the ends furthest from the light source of that tissue (see ref. 4, journal frontispiece). These characteristics are compatible with a cylinder showing internal reflection but are unexpected for a cylinder simply scattering light along its length. A quantitative comparison of axial light transmission through hydrated cylinders of materials known to scatter light or to scatter and reflect light shows that etiolated oat tissue transmits light axially far better than would be expected of a simple scattering agent (not shown). Among several materials tested, a hydrated, tightly rolled cylinder of polyethylene (Saran Wrap) transmitted roughly 10-fold more light axially than did other paper materials known to scatter light but was roughly 1/10th as effective in transmitting light as was a segment of etiolated oat tissue of equal length and diameter (not shown).

How Efficient Are Etiolated Organs as Wave Guides? Of the tissues measured, mesocotyls were the most effective as light guides. However, they were only about 10, 2.2, and 0.7% as effective as a glass rod, 1% agar (which here, is optically equivalent to a column of water), and an optical fiber, respectively (Table 1). Mung bean hypocotyl hook regions were least effective in axially transmitting light, being 1.3% as effective as oat mesocotyl. The relative efficiency of all the tissues is probably underestimated because the nontransmitting cell walls and vasculature were included in the calculation of the cross-sectional areas of the tissues (see ref. 4, journal frontispiece).

Tissue age is apparently a major factor in the efficiency of tissue light-guiding. Oat coleoptiles 4 and 5 days old were 13.5 and 32.4% as effective, respectively, as oat mesocotyl; the older the tissue, the more elongated the cells in that tissue and the more efficient is the axial light transmission by the tissues. This point is also shown by the different regions of the mung bean hypocotyl examined (Table 1) which ranged from young, iso-

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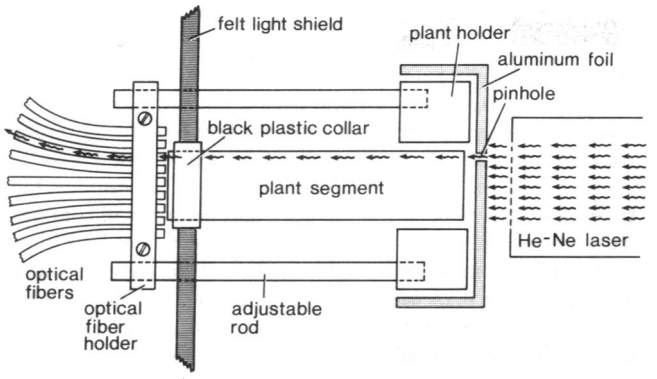

FIG. 1. The patterns of light across the tissue(s) when a narrow laser beam was applied to them was sampled by an array of optical fibers. The plant tissue segment was inserted into a holder which allowed illumination of one cut end; the opposite end of the tissue was abutted to a linear array of optical fibers, each 0.25 mm in diameter (Crofon 10-mil fibers, Edmund Scientific, Barrington, NJ). The distance between the optical fiber holder and the plant holder was adjusted with two rods on which the optical fiber holder could slide. The fiber ends were flush with the optical fiber holder; they are diagrammed here as protruding from the holder for illustrative purposes. The light carried by each fiber was measured separately with a photomultiplier (not shown). These fibers were shielded from stray light by a black plastic collar and a felt shield that fitted snugly over the end of the plant segment adjacent to the optical fibers.

diametric cells in the hook to mature, elongated cells toward the root (5).

Are Etiolated Organs Analogous to a Single-Fiber Optic or a Multifiber Optic Bundle? Internal reflection occurs in a medium with a refractive index (η) higher than that of its surrounding medium. If these etiolated organs are analogous to a single-fiber, optical wave guide, then changing the η of the external medium, normally air, relative to the internal medium, the tissues themselves, should alter light-guiding by the organ. When external and internal η values are equal, light-guiding should be eliminated. Alternately, if these organs are best described as a multifiber optic bundle, changing the η of the outside of the organ relative to the inside should only affect those fibers on the periphery of the bundle. Values of η are 1.0003 for air, 1.3330 for water, 1.4445–1.4380 for wax, and 1.515 for immersion oil at 20°C (6).

Abrasion of the cuticle of oat mesocotyl and coleoptile with emery powder slightly decreased the tissue diameter but did not alter the amount of light guided per mm for either tissue (not shown). Therefore, it is unlikely that the cuticle provides an outer refractive surface. The cell contents are the most likely internal medium through which light actually travels because cell walls and vasculature appear dark relative to the cell interior (see ref. 4, journal frontispiece). Hence, η of the internal medium is approximately that of water, 1.3330. Placing a strip of agar on one side of a segment of etiolated tissue increases the effective η of the outer medium and thus roughly equalizes the inner and outer η values. Similarly, coating the exterior of the unabraded tissues with immersion oil would increase the η of the external medium above that of the tissue significantly. Also, more light will travel in the oil coating now because the plant/oil η values match better than do the η values of the plant/air interface. Therefore, axial light transmission should disappear in a single fiber and only decrease in a multifiber optic system.

For all tissues tested except mung bean, an increase in the effective η of the outer medium resulted in a decrease but not a complete loss of the axial light transmission (Table 2). Inclusion of a light absorber (lamp black) in the oil used to coat the tissue exteriors further reduced axial light transmission in these organs. This loss may be attributable to absorption of light which might otherwise have been reflected back internally from the outer surface of the tissue.

Single and multiple fiber optic systems also behave differently when dissected. A single-fiber optic will cease light-guiding and scatter light from the ragged surface created when halved longitudinally whereas a multifiber optic bundle will lose only half its optical fibers and hence should continue to guide half the light transmitted before dissection. All the tissues tested showed a 50–60% reduction in axial light transmission when halved longitudinally (Table 2).

Do These Tissues Have an Angular Dependence for Acceptance of Light? Fiber optics can only reflect internally that light which impinges on the plane surface of the end of the fiber at or below a certain critical angle (degrees from normal). Classical geometric optics say that this critical angle is a function of the η values of the inside and outside of the wave guide. Multifiber optical bundles or single-fiber optics illuminated from the side also display angular dependence of the light they can capture and guide, but the acceptance angle of the more complex optical system does not depend solely on the critical angle of the individual fibers (7). Hence, the acceptance angle of a multifiber optic bundle is not necessarily the same as the critical angle of the individual fibers of which it is composed.

Attempts at a conventional measurement of the critical angle by applying the laser to the severed end of the tissues were unsuccessful. Rather, the tissue showed the behavior of a light-guide receiving light through a scattering surface (Fig. 2 *Left*). A true scattering surface alone should show transmission as a cosine function of the incident angle. Tissue damage results in

Table 1. Axial light transmission by materials that internally reflect light and by etiolated tissues

	Cross section,* mm^2	Light transmitted, log (units/mm^3)
Glass rod	3.24 ± 0.02	4.62
1% agar cylinder	1.42 ± —	5.27
Fiber optic	0.81 ± —	5.81
Oat tissues:		
Mesocotyl	0.88 ± 0.04	3.62
Coleoptile, 4 days old	0.97 ± 0.03	2.75
Coleoptile, 5 days old	0.97 ± 0.03	3.13
Mung bean:		
Hook region	1.09 ± 0.08	1.74
Upper hypocotyl	3.27 ± 0.13	2.65
Lower hypocotyl	4.22 ± 0.12	2.80
Hypocotyl to root	3.58 ± 0.17	3.16
Corn:		
Root	1.00 ± 0.04	3.51

* Shown as mean ± SEM.

Table 2. Altering the surrounding η or dissecting the tissues to determine if they are single or multiple fiber optics

	Transmission,* %			
	Oat mesocotyl	Oat coleoptile	Mung bean hypocotyl	Corn root
Intact, air	100 ± —	100 ± —	100 ± —	100 ± —
Intact, half in:				
Agar	80.3 ± 1.8	86.1 ± 1.1	87.1 ± 3.4	86.1 ± 0.8
Clear oil	63.6 ± 2.2	52.0 ± 5.6	101.2 ± 2.6	79.0 ± 1.7
Black oil	44.1 ± 2.0	64.4 ± 4.5	64.1 ± 3.0	75.6 ± 2.7
Halved longitudinally:				
In air	42.9 ± 2.0	40.4 ± 3.0	56.7 ± 4.3	50.1 ± 2.7

* Shown as mean ± SEM.

light scatter at sites of damage such as crushed regions or cut surfaces of tissue segments (4). Reduction of light scatter along the exterior of tissue segments by coating the tissue with absorbant black oil reduced the total amount of axially transmitted light from 100% to 44–76% (Table 2) but did not significantly change the shape of the curves obtained when laser light was applied to the cut ends of the tissues (Fig. 2 *Left*).

Acceptance angles of the tissues could be assessed when undamaged tissue surfaces were illuminated (Fig. 2 *Right*). Acceptance angles are conventionally expressed in degrees from normal with respect to the irradiated surface. Axial light transmission by plant tissues is strongly angle-dependent when the incident angle of the laser, with respect to normal, is varied. Also, the angle at which the most light-guiding is found and the shape of the curve describing this angular dependence appear to be characteristic for each plant species examined. Etiolated bean hypocotyl has an acceptance angle of 47° whereas oat and corn have acceptance angles of 59° and 52°–54°, respectively (Figs. 2 *Left* and 3). Although the shapes of these curves are different for each species examined (e.g., oat mesocotyl versus corn root), the shapes of the curves for different tissues from the same species (e.g., oat coleoptile and mesocotyl or corn coleoptile and root) are similar.

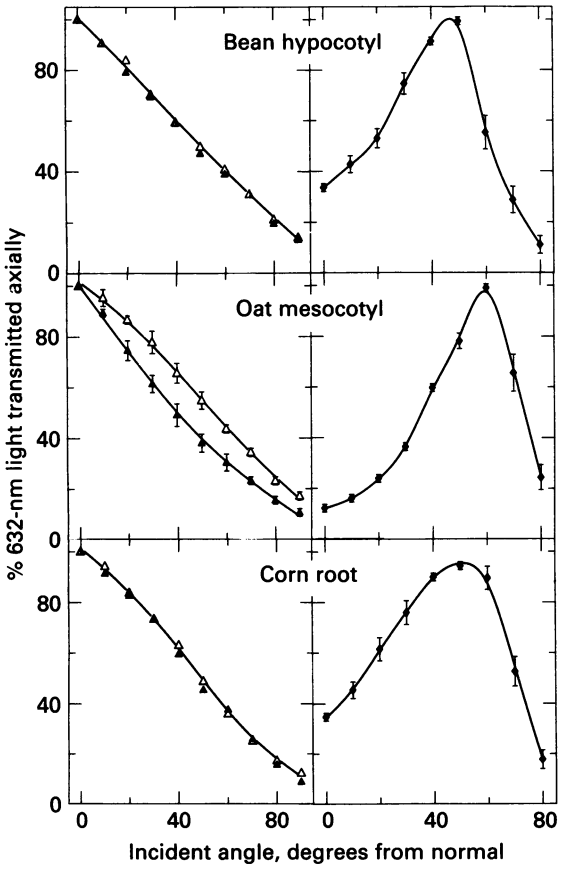

FIG. 2. (*Left*) The critical angles of the cut ends of mung bean, oat, and corn were assessed when the tissues were uncoated (△) or coated with an immersion oil/lamp black paste (▲). (*Right*) The tissue acceptance angle when laser light was applied to a bent, intact seedling a fixed distance from the cut end which abuts the photomultiplier (◆). These distances were 25, 15, and 15 mm for mung hypocotyl, oat mesocotyl, and corn root, respectively. This tissue was coated with oil/lamp black paste except for the region to which the laser beam was applied. SEMs (n = 10–12) are omitted in some panels only for the sake of clarity. One hundred percent was taken as the maximum transmission obtained for illumination of either the cut end or the side of the tissue.

Are Etiolated Plant Tissues Optically Coherent? Multifiber optic bundles are considered to be coherent if they can transmit an image faithfully from one end to the other. The optical coherence of mung bean, oat, and corn tissues was examined by introducing a narrow pencil of light at one end of the tissue segment and measuring the pattern of the light output across the tissue at the opposite end with a linear array of fiber optics (Fig. 1). With no tissue between the laser and the array of commercially made fibers, the laser output was spread over four fibers (or 1 mm) with most of the light conducted through just one of those fibers (or 0.25 mm) (Fig. 4). Because laser light is collimated, this pattern in the absence of any tissue serves as a control for all tissue lengths used. As pieces of tissue of increasing length were placed between the laser and the fiber optics, the total area under the curves, or the lateral divergence of the laser beam as it passes through the tissue, increased (Fig. 4*A*). This increase represents the lateral "cross-talk" between parallel optical units in the plant. Areas under these curves were compared by weighing paper cutouts from photocopies of each curve. The maximal output of a single fiber for each tissue length has been normalized to 100% (fiber no. 9) and the baselines for each curve have been vertically displaced.

For tissue segments 0, 10, 15, and 20 mm long, the total area under the curves increased from 100% to 196%, 241%, and 248%, respectively. About 40% of this lateral divergence for tissue segments 15 and 20 mm long apparently is the result of a scattering artifact at the cut surface of the tissue because the tissue is not wide enough to extend to the fibers where this light was measured (Fig. 4*A*). Despite this artifact, it is clear that the mung bean hypocotyl, as measured here, is a remarkably coherent multifiber optic system over at least 20 mm such that a laser beam measured over approximately 5.3 cell diameters (fibers 9 and 10 with 0.10 ± 0.02 mm as measured cell diameter, n = 50) does not spread laterally to the other side of the tissue, 20 cells away.

Oat mesocotyl, coleoptile, and corn root also apparently are capable of coherent information transfer (not shown). This assessment of tissue optical coherence is hampered by the fact that the tissues used could not be bent because of technical difficulties with the fiber optic device (Fig. 1). Thus, although naturally curved tissue segments were selected, the possibility that part of the pattern obtained was a result of direct laser illumination of the fibers could not be eliminated. Therefore, the light pattern was measured at the end of the tissue when the laser was applied to the side of the tissue at 0°, 40°, and 80° from

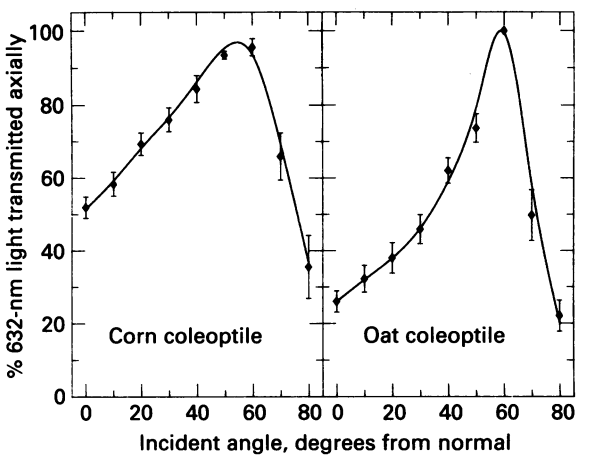

FIG. 3. Tissue acceptance angle of corn and oat coleoptiles. Details as for Fig. 2 *Right*. Distances were 15 mm for both oat and corn coleoptiles.

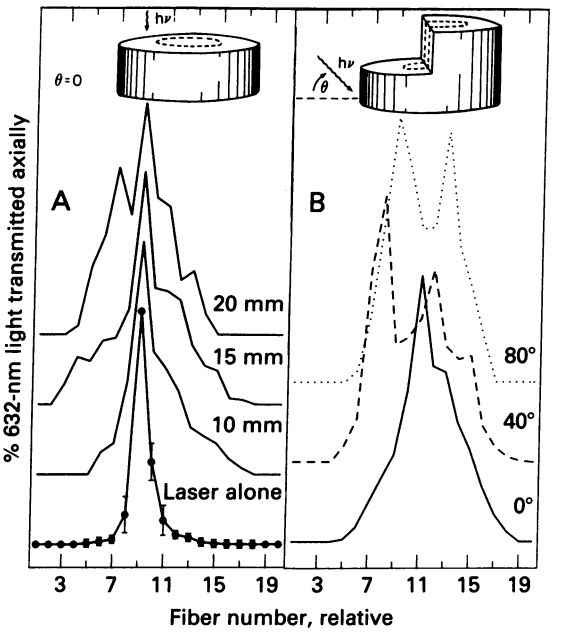

FIG. 4. Lateral divergence of light through the tissue when a narrow laser beam was passed through a pinhole in an aluminum foil shield (Fig. 1) into the end of different lengths of tissue. Lateral divergence of light in mung bean tissue segments (for segments 10, 15, and 20 mm long) when the laser was applied to the cut end of the tissue (*A*), or to the side of the intact seedling about 10 mm away from the optical fibers (see Fig. 3) at the angles specified (*B*). Angles are expressed in degrees from normal with respect to either the cut end (*A*) or the side of the tissue (*B*). Lines connect means of measurements made on three separate segments or seedlings. Mean tissue diameters (± SEM; $n = 50$), 2.66 ± 0.16 mm, have been converted to numbers of fibers covered in diagrams *A* and *B*. Error bars show SEM when $n \geq 9$.

normal. Again, these patterns were expressed as a percentage of the maximal output obtained from a single fiber, and the curves are vertically displaced from each other for clarity. Coherence of the mung bean hypocotyl was seen even with laser illumination at normal incidence (0°) (Fig. 4*B*). As the incident angle was increased, four changes were observed. First, the absolute amount of light axially transmitted increased as the critical angle was approached (Fig. 2 *Right*). Second, the width of the band of light broadened as measured at half peak height, indicating an increase in lateral light dispersion across the tissue. Third, a prominent second peak appeared (Fig. 4*B*); this second peak may be related to the position of nontransmitting vascular tissues (Fig. 4*B*; see also ref. 4). Fourth, the position of the peak closest to the light source shifted as a function of the angle of incidence; this peak in axial light transmission was closest to the illuminated surface when the incident beam struck the tissue near the acceptance angle (Fig. 4*B*). Near the acceptance angle, the first fibers intercepting the light will capture and internally reflect it, whereas far from this angle the light must be scattered before it can be reflected longitudinally. Physical interpretation of these four changes is limited by the sampling technique: light emerging from a complex two-dimensional surface is only being sampled in one dimension.

How Does the Coleoptilar Tip Influence the Light Patterns Across This Tissue? The influence of tissue shape or cell arrangement on the pattern can be assessed either at the tip or at a distance from this special structure because we know that longitudinal light transfer is coherent (Fig. 4).

Laser illumination of an excised coleoptile tip normal to the long axis of the seedling showed clearly that the "lighted" side of the tip was brighter than the "shaded" side and created a funnel-shaped pattern on a white surface placed under the tissue. This light pattern is attributable to scatter by the tip and does not support the idea that the coleoptile tip acts as a lens (8–10).

Laser illumination of the coleoptile tip can occur in three ways relative to its shape because the tip resembles a half dome (Fig. 5*A*). Illumination could be (*i*) to the edge or profile of the concave face, (*ii*) to the concave side, or (*iii*) to the convex side of the hemi-dome (see, respectively, arrows 1, 2, and 3 in Fig. 5*A*). The pattern of light produced by this tip illumination was measured 6–8 mm down the coleoptile from the tip. Again, the maximal output of a single fiber on the lighted side of the tip was taken as 100% and the curves are vertically displaced (Fig. 5). Surprisingly, laser illumination of either the concave or convex face of the coleoptile tips produced more light transmission on the shaded side, the side opposite the side being directly illuminated by the laser (Fig. 5, ▲). In oat, roughly twice as much light traveled down the shaded side of the coleoptile (Fig. 5*B*) and in corn, about 3 times more light emerged from the shaded side (Fig. 5*C*) than from the lighted side of the tissue. Illumination of either the concave or convex face of the dome produced nearly identical curves in both tissues (Fig. 5 *B* and *C*; and not shown). When the edge or profile of the convex face was illuminated (Fig. 5*A*, arrow 1) roughly the same amount of light traveled down the two sides of the coleoptile (Fig. 5 *B* and *C*).

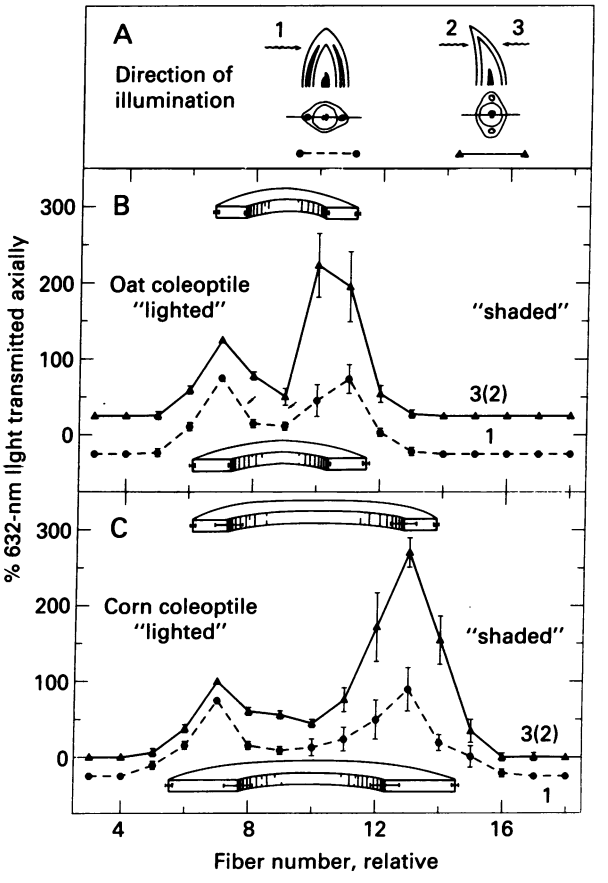

FIG. 5. Pattern of light across the cut end of a coleoptile segment created when only 0.5–0.75 mm of the coleoptile tip was illuminated normal to the tissue longitudinal axis. Solid and dashed lines (*B* and *C*) show light patterns in the coleoptile when different faces of the tip were illuminated (as in *A*). Mean tissue dimensions ($n > 22$) ± SEM have been converted to numbers of fibers covered in diagrams in *B* and *C*. Cell diameters were measured at ×100 with a calibrated ocular micrometer. Tissue diameters were measured with a Helios caliper (Brookstone, Petersborough, NH).

The illustrations of the position of the corn and oat coleoptiles relative to the pattern of light emerging from the tissues (Fig. 5 *B* and *C*) confirm visual observations that light is traveling through the coleoptile and not through the primary leaves (see ref. 4, journal frontispiece). The individual optical fibers in the sampling device average the light output of the leaf and coleoptile tissue with the light output of the spaces between these tissues, and each datum point is the mean of 8–10 individual plants which vary in dimensions of the coleoptile and arrangement of the primary leaves. Hence, the relative amount of light measured for the spaces between the leaves is underestimated and that measured for the leaf axial light transmission is overestimated. The relationship between the coleoptile inner to outer cross-sectional areas is constant ($y = 1.81x \pm 0.55$, $r^2 = 0.84$ for oat; $y = 1.42x \pm 1.63$, $r^2 = 0.80$ corn; y is the outer and x is the inner cross-sectional area).

DISCUSSION

An understanding of optical properties has led to some fascinating discoveries about the way organisms perceive light (e.g., refs. 11 and 12). In filamentous organisms such as *Phycomyces*, optical properties of the reproductive structures play an important role in the success of spore dispersal, allowing the fungus to orient its sporangiophore toward light (9, 12–15). The same type of lens effect has been seen in unicellular algae (e.g., ref. 16) and moss chloronemata (17). In the rhabdomere of the fly, light-guiding sharpens visual resolution (11) and modifies aspects of color vision (18).

We have established that internal reflectance occurs in various multicellular plants and have shown, within the limitations of these measurements, that these tissues are analogous to coherent multifiber optic bundles. Each tissue displays an angular dependence or acceptance angle that is characteristic for a given plant.

Some physiological consequences of this optical property have been discussed (4). In etiolated oats, potential sites of photoperception could be localized only after the light piping properties of the tissues were known. Light-guiding by the oat coleoptile and mesocotyl effectively increases the surface area over which light could be collected; hence, the fluence required to stimulate a given magnitude of photomorphogenesis was decreased. This effect was underestimated in previous calculations (4); the equation derived in those calculations which quantitatively described light-guiding by the tissues was applicable to light only at normal incidence. In fact, at 59° from the normal, 75–85% more light will be collected and guided through the tissue than at an incident angle of 0° because of the angular dependence of light-guiding in oat tissues (Fig. 4).

Although light gradients in multicellular plant organs have been postulated and the physiological significance of these gradients has been discussed (9, 19–21), to the best of our knowledge, the existence of such gradients has not been directly documented (cf. ref. 22). It is enticing to speculate on the physiological impact of these unexpected light patterns across the tissue which have been generated by the coleoptile tips of corn and oats (Fig. 5), particularly in regard to phototropic phenomena. The most plausible explanation for the increased amount of light traveling down the shaded side of the coleoptile is that, because the cell files from either half of the coleoptile converge and form arcs at the tip (23), they are receiving light at an angle closer to their best acceptance angle. The light they collect is then preferentially internally reflected around the coleoptile tip and down the shaded side. It should be pointed out that the gradients shown here pertain only to the quantity of light traveling down the sides of the tissue and does not describe the relative amounts of light on the lighted and shaded sides of the tissue at the coleoptile tip itself.

Convergence of light on the shaded side in single cells, such as *Phycomyces* in which the cell acts as a lens, is well accepted (12, 15) but has been disputed in multicellular organs such as oat coleoptile tips because a similar optical lens effect produced by the tip itself was deemed impossible (see discussion in ref. 13; cf. ref. 24). Our observations on the laser-illuminated coleoptile tip indicate that it is not acting as a lens that focuses light on the shaded side of the tip itself. Shropshire (8) was able to reverse the direction of phototropic curvature of oat coleoptiles by placing a lens in front of the tip. He concluded that the coleoptile tip itself acts as a lens normally focusing light on the shaded side but that this effect was destroyed when the glass lens was interposed because the light beam striking the tissue was too highly divergent for the tissue to refocus. In view of the present data on the optical properties of the coleoptile tip, this may be too simple an explanation.

The consequences of the optical properties of etiolated tissues cannot be fully addressed until the wavelength dependence, critical angle(s), and path of light through the tissues are known. However, earlier work purporting to show localization of the photoreceptor itself to the extreme tip of the coleoptile (24–26) must also be reevaluated in view of the light-guiding properties of these tissues. Only then can further optical analysis [e.g., analysis of the occurrence of two peaks of transmittance when bean hypocotyl is illuminated laterally at 40° and 80° (Fig. 4*B*)] be approached and the physiological ramifications of the optics of etiolated tissues be fully appreciated.

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