TROPISTIC RESPONSES OF ZYGOTES OF THE FUCACEAE TO POLARIZED LIGHT[1]

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In 1934, Castle [5] reported that a beam of vertically vibrating light[2] needed to be about 10 per cent more intense than an oppositely directed beam of horizontally vibrating light in order to nullify the latter's tendency to effect phototropic bending of an upright *Phycomyces* sporangiophore. This finding of *polarotropism*, an orientation of growth by the polarization of light, was unique; for previous claims [1, 22, 24] were and remain entirely unconvincing and unconfirmed. Castle interpreted the polarotropic response as arising from differential external reflection. This view now seems incorrect [17]; but so viewed the phenomenon revealed nothing and was not pursued.

Recently, I found a striking polarotropic response of *Fucus* zygotes [16]. Zygotes treated with plane polarized white light coming from both above and below tend to germinate horizontally and in the plane of vibration.

I have here tried to study whether or not the polarotropic response of the zygotes is a variant of their response to unpolarized light. For it might not be; the polarized irradiation might orient growth by directly aligning molecules—a hypothesis which invites examination despite the want of evidence for it.

MATERIALS AND METHODS

Obtaining zygotes.—Receptacles, or fertile fronds, of *Fucus furcatus* were collected at Carmel Point, Carmel, California; those of *Pelvetia fastigiata* at Reef Rock, La Jolla. They were treated and stored as described by Whitaker [33] and Jaffe [15], respectively. Three to six days after collection, the receptacles were transferred to a room held at $15 \pm 3/4$°C where all subsequent operations were carried out; these started immediately with a treatment used to stimulate gametangial liberation.

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[2] The direction of vibration here is that of the electric vector.

For *Fucus*, Whitaker's method [33] of simply immersing the stored receptacles in 15°C sea water sometimes failed in these experiments. For this reason, the following further expedient was resorted to: About one hour after immersion the receptacles were placed about two inches below a 20 watt white fluorescent lamp; marked shedding ensued one to three hours later. The treatment for *Pelvetia* has been described [15].

The receptacles of *Fucus* and of *Pelvetia* were discarded about 45 and 15 minutes respectively after shedding began. It was at about this time of discard that 50 per cent of the egg-bearing capsules were estimated to have broken down. This estimated time was taken as the "time of fertilization". Where illumination proved necessary in subsequent operations, only ruby lamps were employed.

The sexual products were allowed to remain in the dark for about 20 minutes after discard so as to complete the dissolution of the öogonial capsules and the fertilization of the eggs. The zygotes were then thoroughly washed with artificial sea water [16] and suspended in the same medium to form a "stock suspension".

Method for vertical illumination.—The central light source was a 500 watt projection lamp powered through a voltage stabilizer. Most of the infrared component was filtered out of the horizontally emanating light by immersing the lamp in the center of a 0.6 molar ferrous sulfate solution held in a glass cylinder; each horizontal beam traversed 37 mm of this filter before emerging. The filter was water-cooled during lamp operation and adequately protected against oxidation by a layer of mineral oil above it, 0.05 molar H_2SO_4 in it and a piece of brass at its bottom.

Horizontal beams from the central light source traversed windows in each of nine boxes; thence they were deflected downward by 45° prisms through appropriate filter trains so as finally to irradiate each of nine egg-bearing culture dishes with two 17 millimeter square patches of plane polarized approximately monochromatic light of known intensity. The filter train in each box consisted of the following components (starting with the one nearest the light source): (i) An over-all Wratten neutral filter (fine adjustment was provided by changing the distance between the light source and the optical box). (ii) An interference filter. The transmission peaks and half band widths used are listed in Table I. (iii) One or more cut-off filters. (iv) Two 17 mm square windows, one being covered by Wratten neutral filters, whose measured transmission was 10 per cent. (v) A Polaroid type H linear polarizing filter.

The intensities impinging on the eggs in each patch of light were measured by replacing the culture dishes with a suitably masked photronic cell whose output was read off a stabilized indicating amplifier. The light intensity measured as reaching a patch via the window *not* directly above it never exceeded 3 per cent of the total reaching it. The photometric setup was calibrated in relative energy terms by comparing its reaction with that of a thermopile (whose output was read off a galvanometer) to light beams of the same spectral composition used in treating the eggs. Tests using appropriate extra filters showed that the light beams used were free of infrared. The absolute energies used were determined by calibration with a Bureau of Standards lamp.

Method for horizontal illumination.—The light source for the lower intensities used was a 15 watt, 6 volt tungsten filament lamp. Its image was focused through 9 cm of 0.04 *M* $CuSO_4$ + 0.04 *M* HCl onto a 1 cm square of white paper. This then acted as a secondary source of white light free of infrared and of polarization. For doses of 10^{18} quanta/cm^2 or greater, the source was changed to a 30 watt sealed spot lamp

TABLE I. *Response of* Fucus *zygotes to monochromatic plane polarized light coming from above.*

The dose is expressed as quanta/cm². For all values of $V_2 \geq 44$ %, the per cent of outgrowths classified as up averaged 1.0 ± 0.8; for 12 % $< V_2 < 44$ %, per cent up = 3 ± 2 %; for $V_2 < 12$ %, per cent up = 8 ± 5 %.

Peak λ (mμ)	Half band width	Egg batch	% bipolar alignment, V_2, for dose of:			% twins for dose of:		
			10^{18}	10^{17}	10^{16}	10^{18}	10^{17}	10^{16}
393	14	a		55±5	44±6		23±4	10±3
		c		61±4	31±6		25±4	16±3
425	9	a		60±4	61±4		30±4	14±3
		c		64±4	49±4		31±4	28±3
436	9	a		71±4	63±4		26±4	22±4
		c		64±4	59±4		22±3	20±3
454	10	c		62±4	57±4		24±4	14±3
459	9	a	67±4	61±4		24±5	46±5	
		c		75±3	60±5		43±4	19±4
483	9	a	80±3	63±3		35±5	36±5	
		c		78±3	61±4		29±4	22±3
499	12	a	77±3	73±3		40±6	35±5	
		c		60±4	42±5		20±3	10±3
522	9	a	65±4	30±7		34±5	8±3	
		b	65±4	37±6		12±3	8±3	
		c	62±4	25±6		25±4	14±3	
546	8	a	12±7	−6±7		4±2	7±2	
		c	21±6			8±2		
567	17	a	33±6	17±8		7±3	6±3	
		b	27±7	8±7		3	3	
579	4	b	−11±7	9±7		0	2	
605	13	b	−1±7			2		
627	16	b	−2±7			0		
650	8	b	−1±7			0		
662	9	b	2±8			0		
690	13	b	−2±7			2		
710	13	b	−19±6	−5±7		3	2	
Dark		a		0±7			4±2	
		b		−9±7			2	
		c		−1±6			14±3	

without a depolarizing paper in its beam. The test eggs lay in horizontally placed rectangular chambers made of microslides. A beam from the source traversed a Polaroid H filter and/or a Wratten neutral filter where appropriate, descended upon one side of each chamber at about $5\frac{1}{2}°$ to the horizontal, and passed through a window so as to illuminate directly only the bottom of the chamber, whence it was totally reflected. Thus each egg was illuminated by two beams whose resultant direction was exactly horizontal. It is estimated that no more than 1 per cent of the "unpolarized" light used in some cases was polarized by reflection before striking the eggs. Light intensities were mainly regulated by changing the distance between the chamber and the source, and were measured using a photronic cell calibrated against a thermopile. On the basis of the emission spectrum of a 2780° K tungsten filament lamp [32] and a measurement of the filter's transmission spectrum, it is estimated that about $\frac{1}{5}$ of the radiant energy striking the eggs lay between 400 and 500 mμ, virtually all the rest lying in the longer wavelength visible.

Analyzing outgrowth directions.—Tenfold magnified shadowgraphs were made of all cultures four days after fertilization. The initial angles of rhizoidal outgrowth as projected in the horizontal plane, or plane of the shadowgraph, were then measured. For the experiments with vertical and equatorial illumination, this analysis was restricted to those embryos whose original centers lay more than 380 mμ or about five egg diameters from their nearest neighbors. In cases where an outgrowth had originated so close to the top of a zygote as to entirely hide its thickened origin, it was classified as "up".

RESULTS

Alignment within the plane perpendicular to the direction of illumination.—As previously reported [16] the polarotropic response was effected by illumination coming from both above and below. A subsequent exploratory experiment showed a similar response to illumination from above only. With this in mind, the effects of treating *Fucus* zygotes before germination with different wavelengths of polarized light coming from above only were investigated. One resultant distribution of outgrowth angles is plotted in Fig. 1 *a*.

To characterize the degree of bipolar alignment of each measured distribution, the parameter, V_2 was calculated [7]:

$$V_2 = \Sigma p \cos 2\theta,$$

where p = the percentage of all outgrowths whose projection in the horizontal plane originated at an angle θ to the vibration axis. (Outgrowths classified as up were omitted in the calulation of V_2.)

Note that for a distribution perfectly aligned in the vibration axis, $V_2 = +100$ per cent; for one perfectly aligned perpendicular to this axis, $V_2 = -100$ per cent; for a uniform distribution, $V_2 = 0$ per cent; for a random distribution, $V_2 = 0 \pm 70 \times 7$

per cent/$\sqrt{N}$, where N is the total number of outgrowths not pointing up [27]. The "vector method", using V_2, extracts much more information from the data than one of simply dividing it into the two categories, $-45°$ to $+45°$ and $+45°$ to $+135°$. Theoretically, it would require the measurement of two to four times as many angles (as V_2 varies from 0 to 80 per cent) to attain the same accuracy with a two category method as with the vector method (see below). The theoretical variances of V_2,

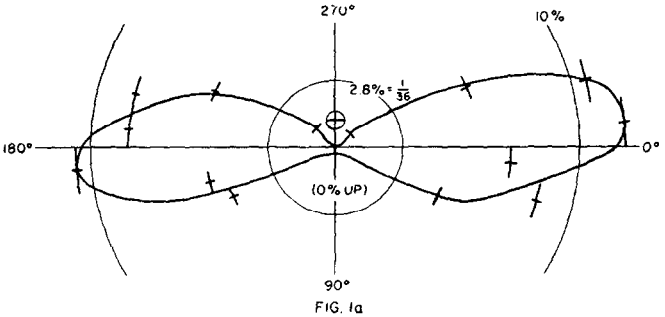

FIG. 1a

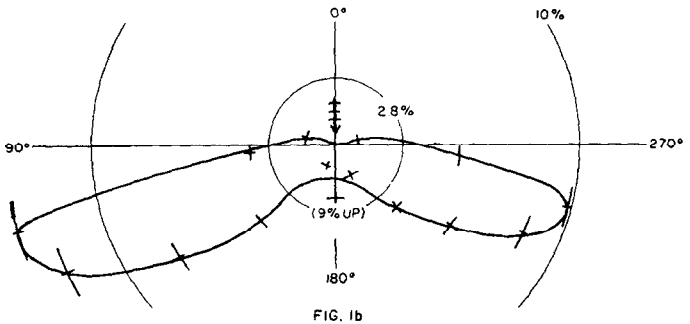

FIG. 1b

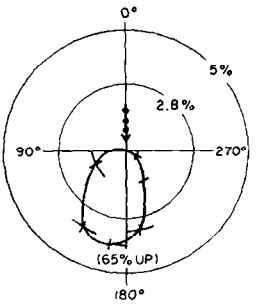

FIG. 1c

Fig. 1.—Illustrative distributions of outgrowth directions of *Fucaceae* eggs in response to treatment with plane polarized light. Per cent of all outgrowths per 10° interval plotted vs. angle. 1*a*—*Fucus* eggs treated with 10^{17} quanta of 483 mμ polarized light coming from above (egg batch c). 0°–180° axis marks plane of vibration. $V_2 = 78$ per cent; $\theta_2 = 0.5°$; $V_1 = 6$ per cent. 1*b*—*Pelvetia* eggs treated with white light horizontally polarized and coming horizontally in the direction of the arrow. 10^{17} quanta of the light lay between 400 and 500 mμ. 1*c*—Same as 1*b* except vertically polarized.

$\sigma(V_2)$, were read off a plot of $\sigma(V_2)$ vs. V_2 constructed for circular normal distributions. These have the form [13]:

$$F(\theta) = \frac{e^{K \cos 2\theta}}{2\pi I_0(K)},$$

where K is a parameter characterizing the degree of alignment.[1] The graph was made using the following two characteristics of circular normal distributions, taken from

[1] $I_0(K)$, $I_1(K)$, and $I_2(K)$ are Bessel functions of the first kind of pure imaginary argument.

Gumbel *et al.* ([13], p. 139) and from Greenwood and Durand ([12], p. 236) respectively:

$$V_2 = I_1(K)/I_0(K)$$

$$\sigma(V_2) = \frac{1}{\sqrt{N}} \cdot \sqrt{\frac{1}{2} + \frac{I_2(K)}{2\,I_0(K)} - \left(\frac{I_1(K)}{I_0(K)}\right)^2}\,.$$

Evidence that the circular normal distribution is an adequate model is provided in Fig. 2. In order to reveal the shape of the empirical distributions, the largest possible sample was obtained as follows: Those eight distributions for which V_2 happened to lie between 60 and 62 per cent were pooled. Furthermore, each group of four symmetrical ten degree intervals (e.g. 0–10°, 170–80°, 180–90°, and 350–60°) were pooled. In Fig. 2, the histogram represents this empirical data and the smooth curve is taken from that circular normal distribution for which $V_2 = 61$ per cent.

The main result of this investigation appears in Fig. 3*a*, where the bipolar alignment parameters, V_2, are so arranged as to allow the drawing of an action spectrum. The doses employed in all the treatments whose results are listed across from a given dosage were equalized within about 10 per cent. Each dose was applied by means of a ten hour long constant intensity treatment starting two hours after fertilization. (Under comparable conditions, the first zygotes are reported to begin germination 10 to 14 hours after fertilization [34].) In Table I, these same data appear together with estimates of standard deviations and other accessory information.

Consideration of Fig. 3*a* and Table I indicates that a maximum of sensitivity of the eggs toward the growth aligning effect lies between 435 mμ and

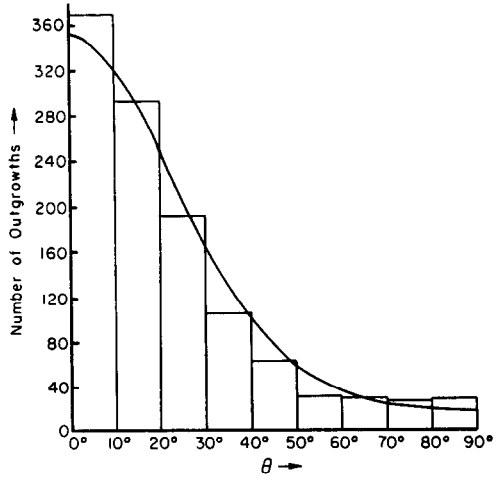

Fig. 2.—Exact shape of distributions of *Fucus* outgrowth directions in response to polarized light coming from above.

490 mμ. In this region the total dose required to produce 60 per cent orientation is 10^{16} quanta/cm^2 which is 4×10^4 ergs/cm^2 at 480 mμ. The sensitivity falls relatively slowly toward short wavelengths; at 400 mμ it is about 1/10 maximal. But it falls precipitously toward long wavelengths; at 522 mμ,

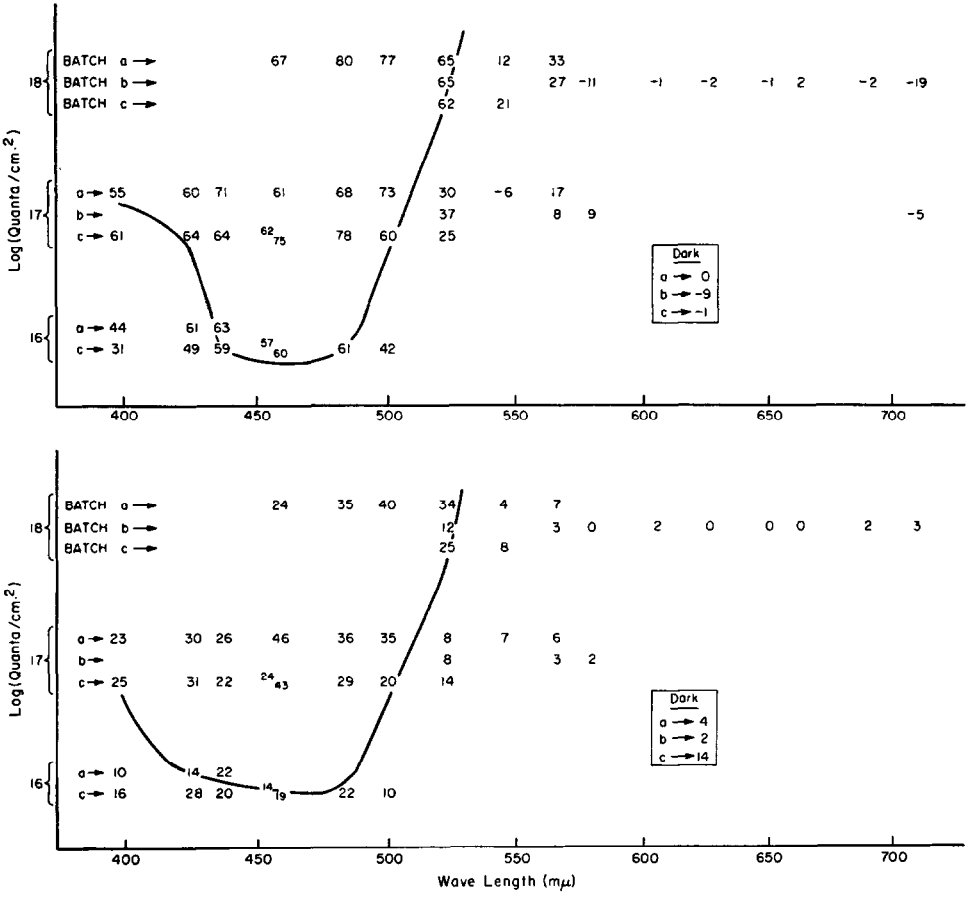

Fig. 3.—Wavelength dependence of response of *Fucus* eggs to plane polarized light coming from above. Fig. 3*a* (above): Alignment response, V_2. The curve is drawn through interpolated doses giving 60 per cent alignment. Fig. 3*b* (below): Twinning response. The curve is drawn through interpolated doses giving 25 per cent twinning.

it is about 1/100 maximal; at 546 and 560 mμ, no more than 1/1000 maximal; between 579 and 710 mμ, no more than 1/10,000 maximal.

It has been assumed that the central tendency of the outgrowths is exactly 0°. Analysis of the present data establishes this point with considerable preci-

TABLE II. *Evidence that outgrowth distributions lack any unipolar component.*

	Strong bipolar orientation ($V_2 = 60 - 80$ %)	Weak bipolar orientation ($V_2 = -20$ to $+20$ %)
Empirical $\sigma(V_1)$	7.0 %	5.9 %
Expected $\sigma(V_1)$	7.7 %[b]	6.9 %[a]
Empirical $\sigma(W_1)$	3.5 %	6.2 %
Expected $\sigma(W_1)$	3.5 %[c]	6.9 %[a]

[a] From Rayleigh distribution [27].
[b] Weighted average between Rayleigh and binomial distributions.
[c] For a mixture of independent Rayleigh and binomial distributions.

sion. The central tendency of each distribution was first characterized by the parameter:

$$\theta_2 = \tfrac{1}{2} \arctan\left(\frac{\Sigma p \sin 2\theta}{\Sigma p \cos 2\theta}\right).$$

The results were then averaged for all 22 distributions which showed at least 60 per cent alignment, yielding the value, $+0.30 \pm 2.8°$.

Moreover, the above data concerns a tendency to grow out either in one direction or its opposite. In view of the symmetry of the known directive influences—light vibration plane, light direction, substratum plane, and residual group effects—it is to be expected that there will be an equal tendency to develop in any two opposite directions; this too is well confirmed by analysis. The requisite information was obtained by first calculating both components of the *unipolar* alignment vector for each distribution:

$$V_1 = \Sigma p \cos\theta, \qquad W_1 = \Sigma p \sin\theta.$$

Table II shows the good agreement between their empirical standard deviations from zero and their theoretical ones as estimated on the basis of random fluctuations.

Alignment within the plane containing the light direction.—Zygotes of *P. fastigiata* were illuminated with white light from one horizontal direction during the period from two to nine hours after fertilization. (Preliminary experiments showed that some zygotes first begin to germinate about 10 to 12 hours after fertilization under similar conditions.)

TABLE III. *Alignment of germination of* P. fastigiata *zygotes by unilateral unpolarized light.*

The dose given is of the estimated fraction of light lying below 500 mμ. 180° indicates germination directly away from the light; 0°, toward it. Outgrowths classified as "up" were not included in the totals. Temperature is 15°C except as noted.

	Dose (quanta/cm²)					
	0	10^{14}	10^{15}	10^{16}	10^{17}	10^{19}[b]
Light on (hrs. after fertiliz.)	[a]	2	2	2	2	1½
Light off (hrs. after fertiliz.)		9	9	9	9	3½
% of outgrowths: 0–90°	47±4	49±5	43±6	19±3	6±2	19±2
90–135°	31±4	29±5	39±6	54±4	43±4	28±3
135–180°	22±4	22±4	19±4	27±4	51±4	53±3
160–180°	11±3	6±2	7±3	10±3	20±3	

[a] Dark control.
[b] $T = 16°C$.

In this case, it is first necessary to consider the response to *un*polarized light. Consider Table III. Compare the dark control with the response to 10^{16} quanta/cm². It will be seen that the response to this intensity is *not* an aggregation of outgrowths in the vicinity of the rear pole, or 180°; rather, it is a tendency to accumulate outgrowths in the *subequatorial* zone between 90° and 135°. At 10^{15} quanta/cm², a weaker, but still significant subequatorial response is seen. However, at 10^{17} and 10^{19} quanta/cm², a rear pole response appears.

In Table IV, find the comparable responses of *F. furcatus* zygotes as reported by Whitaker and Lowrance [34]. 10^{16} quanta/cm² of unilateral unpolarized illumination yields a clear subequatorial response when applied between 9 and 16 hours after fertilization; however, earlier or more intense treatments yield a rear pole response.

The responses to horizontally directed polarized light may now be considered. Fig. 1*b* shows an illustrative outgrowth distribution—that in response to a dose of *horizontally* vibrating light of which 10^{17} quanta/cm² lay between 400 and 500 mμ. Evidently these outgrowths are strongly concentrated around a subequatorial angle. Fig. 1*c* shows another illustrative outgrowth distribution—that in response to the same dose of *vertically* vibrating light. Sixty-five per cent of these zygotes grew "up", the rest tending to

TABLE IV. *As Table III, for* F. furcatus.

(Data of Whitaker and Lowrance [34].)

Dose ...	10^{16}						10^{16}						10^{17}
Light on	[a]	5	6	7	8	9	10	11	12	13	14	15	2
Light off	[a]	6	7	8	9	10	11	12	13	14	15	16	27
0–90°	49±3	38	15	2	5	8	8	10	15	14	23	31	0
90–135°	25±2	28	36	46	52	68	72	66	62	66	62	52	8
135–180°	26±2	34	49	52	43	24	20	24	23	20	15	17	92

[a] Averages of 14 observations of zygotes treated for one hour with 10^{16} quanta/cm² during the *insensitive* periods from 2–15 and 16–27 hours after fertilization. Their tabulated empirical variances appear to be good gages of those of the other figures.

develop directly away from the light. (A zygote cannot grow downward because of the hard substratum.)

Between 10^{15} quanta/cm², the lowest dose eliciting a non-random response, and 5×10^{19} quanta/cm², the highest dose tested, the responses did not differ qualitatively from the above illustrations. Hence, for the purpose of rapidly visualizing the response to plane polarized light over this range, Fig. 1*a*, 1*b*, and 1*c* may be considered as three orthogonal views of the same distribution. In brief, this distribution is shaped like a wing nut; the wings lie in the vibration plane and point at two symmetric subequatorial angles.

Now, to more precisely describe the responses to horizontally directed lights, both polarized and unpolarized, the distributions were characterized by two bipolar parameters: ϕ_2, a measure of central tendency, and L_2, a measure of the degree of orientation around ϕ_2.

$$\phi_2 = \tfrac{1}{2} \arctan \left[\frac{\Sigma [p(\phi) + p(-\phi] \sin 2\phi}{\Sigma p(\phi) \cos 2\phi} \right],$$

$$L_2 = \sqrt{\Sigma [p(\phi) + p(-\phi)] \sin 2\phi]^2 + [\Sigma p(\phi) \cos 2\phi]^2}.$$

where $p(\phi)$ is the percentage of all outgrowths whose projection in the horizontal plane originated at an angle ϕ to the direction of illumination.

ϕ_2 and L_2 are parameters descriptive of behavior in the plane of the light direction corresponding to θ_2 and V_2 in the plane perpendicular to the light direction. For the distribution shown in Fig. 1*b*, $\phi_2 = 115°$ and $L_2 = 70$ per cent. These parameters furnish a somewhat misleading description of the

TABLE V. *Response of* Pelvetia *zygotes to unilateral white light.*

In the experiment using egg batch *A*, 140 to 290 eggs were counted per treatment; for batch *B*, 80 to 150. (Distributions characterized by ϕ values in parentheses are not significantly different from random ones.)

	Quanta/cm² (400–500 mμ)							
	0	10^{14}	10^{15}	10^{16}	10^{17}	10^{18}	5×10^{19}	0
Egg batch ...	*A*	*A*	*A*	*A*	*A*	*B*	*B*	*B*
Polarization:								
Horizontal								
ϕ_2	(102°)	(164°)	106°	111°	115°	117°	128°	(51°)
L_2	6	7	17	52	70	62	76	3
% Up	38	44	44	19	9	20	5	62
None								
ϕ_2	(102°)	95°	104°	122°	137°			
L_2	6	10	21	26	42			
% Up	38	44	45	43	34			
Vertical								
ϕ_2	(102°)	(78°)	125°	137°	152°	145°	169°	(51°)
L_2	6	3	10	16	21	9	31	3
% Up	38	44	47	60	65	85	65	62
ϕ_1	(150°)	(27°)	160°	186°	168°	185°	179°	(245°)
L_1^*	4	4	32	39	71	71	91	9

responses to vertically polarized light since these are unipolar. Hence these latter were likewise characterized by unipolar parameters:

$$\phi_1 = \arctan\left[\frac{\Sigma p \sin\phi}{\Sigma p \cos\phi}\right],$$

$$L_1^* = \frac{1}{1-p(u)}\sqrt{(\Sigma p \sin\phi)^2 + (\Sigma p \cos\phi)^2}.$$

Note that ϕ_1 and L_1^* are measures of the behavior only of those outgrowths not pointing "up". For the distribution shown in Fig. 1 *c*, $\phi_2 = 152°$, $\phi_1 = 168°$, $L_2 = 21$ per cent, and $L_1^* = 71$ per cent.

Now consider Table V in which these characterizations of the responses to horizontally directed light are presented.

Two main points can be extracted from it: (i) The polarized light response and the subequatorial response to *un*polarized light fade out over about the

same intensity range. Fig. 4 shows this economically. In it there is plotted against intensity, a clear measure of the response to the *polarized* character of the light (the difference between L_2 for horizontally and for vertically vibrating light), and a comparable measure of the response to unpolarized light (the difference between L_2 for unpolarized light and the dark control). (ii) The shift with increasing dose of unpolarized light from a subequatorial to a rear pole response is paralleled by a slow drift toward higher angles of the polarotropic response: ϕ_2 increases 22° as the dose of horizontally vibrating light increases 5×10^4 times.

Alignment after equatorial illumination.—*Fucus* zygotes were treated from all directions in a plane with equal doses of unpolarized white light, one third of which lay below 500 mμ. They were exposed at 11°C from 2 to 24 hours after fertilization. In essence the technique was to support the zygotes at the center of a doughnut-shaped fluorescent lamp, with appropriate depolarizing neutral filters and hoop-shaped slits interposed between lamp and zygotes.

The zygotes so treated tended strongly to germinate perpendicular to the plane of illumination. Thus in two cases in which the total dose was about 10^{17} quanta/cm^2, V_2 was equal to 65 ± 9 per cent and 78 ± 7 per cent.

Twinning.—Many *Fucus* embryos developed an outgrowth originating from each of two separate, and usually opposite, regions of the zygote. Such embryos were classified as twins. The percentage of twins as a function of the wavelength and intensity of the polarized light used is presented in Fig. 3*b* and Table I. The action spectrum for this response is readily consistent with that for the alignment effect, but the data are more variable so that the wavelength of maximum effectiveness can be restricted only to the broader region between 410 and 500 mμ.

In this polarotropism study, the *Pelvetia* zygotes never developed two normal outgrowths, though rare embryos showed both a normal and a minute, abortive one. For some entirely obscure reason, in other experiments executed four years before, up to 15 per cent of cultures of *Pelvetia* zygotes sometimes developed into twins.

DISCUSSION

The hypothesis that the polarized irradiation orients growth by directly aligning molecules must be rejected. For two results support what is in any event a simpler assumption—that the orientation of the zygotes' growth by unpolarized and by polarized light are both variants of the general phenomenon of phototropism. First, the zygotes' polarotropic action spectrum (Fig. 3*a*) fits what is known of their tropistic response to unpolarized light

TABLE VI. *Comparison of wavelength dependence (in the visible) of polarotropism with phototropism.*

Phenomenon	Material	Most effective wavelengths	Sensitivity: yellow/peak	Authority
Phototropism	*Phycomyces* sporangiophore	400–460	$\leq 10^{-3}$	Castle, 1931 [4]
,,	*Coprinus* sporophore	400–465	$\leq 10^{-3}$	Boriss, 1934 [2]
,, (low threshold response)	*Avena* coleoptile	435–450, (465–480)[a]	$\leq 10^{-4}$[b]	Johnston, 1934 [18] Curry, 1957 [8] Shropshire, 1957 [29]
Phototropism	*Pilobolus* sporangiophore	430–490	$\leq 10^{-1}$	Bünning, 1937 [3]
Polarotropism	*Fucus* zygote	435–490	$\leq 10^{-4}$ to 10^{-3}	This paper

[a] Secondary peak.
[b] [31].

(it cuts off above 500 mμ for *Cystoseira* [25]), and to all other phototropic spectra (Table VI). Secondly, the polarotropic response and the subequatorial response to unpolarized light fade out over about the same intensity range (Fig. 4).

From a developmental viewpoint, the most revealing residuum is that the polarized light treatment can induce up to half the zygotes to grow into twins. For this implies that the polarity is not established through the rotation of

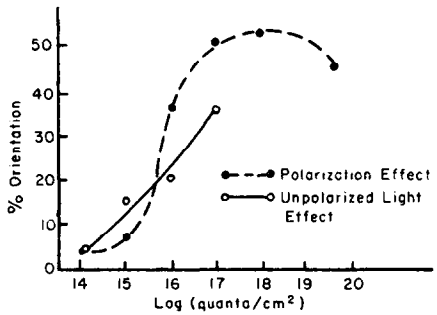

Fig. 4.—Phototropic response of *Pelvetia* eggs to horizontally directed white light.

some preformed asymmetric inclusion, such as the nucleus; it must arise in some more epigenetic manner.

It is also of interest to inquire further into the mechanism of the tropistic responses. First, let us consider the *subequatorial response* to unpolarized

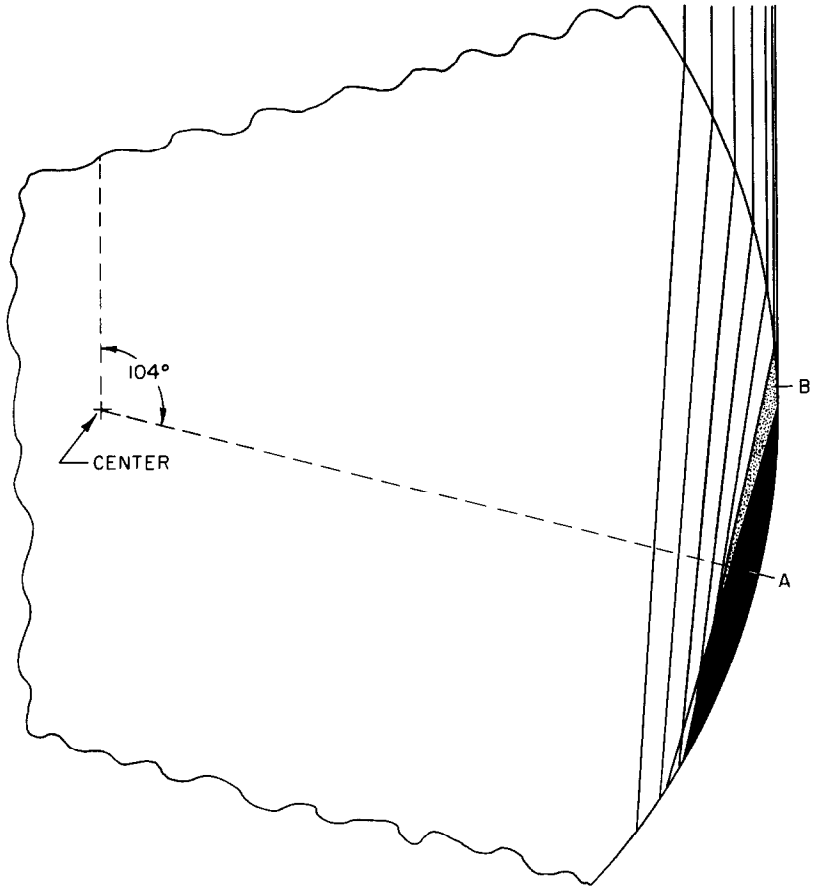

Fig. 5.—Model to show that a shallow subequatorial band in a unilaterally illuminated cell remains dark. Zone *A* is entirely by-passed, while zone *B* receives beams which have lost at least half their energy by external reflection. (Drawn for a spherical cell of refractive index, $n = 1.4$ immersed in a medium, such as sea water, for which $n = 1.34$).

light. Whitaker and Lowrance interpreted both responses as caused by an influence directing growth toward the rear pole; the subequatorial accumulations supposedly resulted from a more intense reorientation of partially determined primordia from the anterior hemisphere to the subequatorial

zone than from the latter region to the rear pole. If this were true, then the concentrations of outgrowths arising near the rear pole would be substantially above the uniform level, even in the most extreme cases; but there, they are, if anything, below this level. (See Table III, 10^{15} and 10^{16} quanta/cm^2; Table IV, illumination started 13 to 15 hours after fertilization.) Hence the subequatorial response must be considered a consequence of a truly subequatorial directive influence.

I can conceive of only one general hypothesis to explain such an influence: Growth is directed toward the subequatorial zone because its peripheral portions are the darkest region of the cell. Consider Fig. 5. Only scattered light reaches the by-passed band (A) at the zone's periphery and under it is a second shallow band (B) heavily shaded by reflection losses. This analysis likewise explains several other facts: (i) Spores of the mosses, *Neckera complanata* and *Amblystegium serpens* grow out at "90°" to unilateral and presumably unpolarized light of low intensities [14]. (Heitz's report is undocumented so it may well be that the response is actually *sub*equatorial.) (ii) The zygotes of four species of *Fucus* [16, 19] as well as spores of *Equisetum* [26] germinate equatorially in response to *bi*lateral illumination. (iii) The zygotes of *F. furcatus* (these results) and the spores of *Equisetum* [26] both grow out at 90° to the light directions in response to equatorial illumination. It should be emphasized that this analysis requires that the effective photoreceptors be concentrated in a surface layer. For those rays which are diverted from the by-passed zone by the cell's lens action are concentrated just beneath the surface (Fig. 5). If photoreceptors were as abundant in this subsurface region as in the more peripheral shell, then it would be most difficult to understand how the net photochemical action in the subequatorial zone could be lower than at the rear pole.

It likewise seems almost inescapable that when the *rear pole response* occurs, the most posterior region of the cell becomes effectually the darkest, but the mechanism of this shift is obscure. Photoreceptor molecules deeper in the cell may come into play, a subtle chloroplast movement may change the pattern of scattering and absorption, or the cell may integrate the incoming information by centering its response at the unique center of the darkest hemisphere instead of some indeterminate point of the darkest ring.

Now consider the mechanism of the polarotropic response. It is a variant of the subequatorial one. Hence in some manner the photoreceptor molecules in those meridians of the subequatorial zone lying parallel to the vibration plane must receive least light, How? Since Fresnel reflection is least effective at the cell surfaces in these meridians, *differential external reflection*

will cause a relatively greater illumination of the preferentially germinating regions and must be rejected as an explanation. Moreover, *differential internal reflection* cannot over-compensate for this effect because following its first internal reflection each ray has not only been weakened by its second reflection, by absorption and by scattering but traverses a region relatively far from the preferentially germinating one.

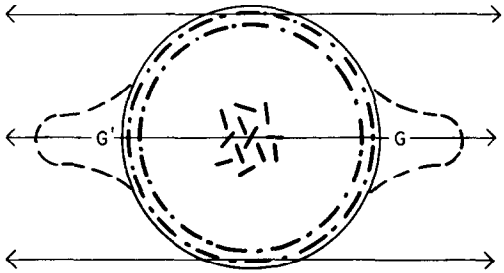

Fig. 6.—Model of egg to show that the photoreceptor molecules in the germinating regions (*G* and *G'*) will absorb least light if the photoreceptors are located near the cell surface and are periclinally oriented. Light enters perpendicular to plane of page, vibrating as shown by double-headed arrows. Dashes within egg represent the axes of maximum light absorption of photoreceptors; dots are photoreceptors lying perpendicular to plane of page; photoreceptors lying between polar and equatorial regions not indicated.

Two possibilities remain: (i) *Differential scattering:* Peripheral molecules in the meridian parallel to the vibration plane are open to substantially less light intracellularly scattered from rays vibrating perpendicular to the scattering plane than the corresponding molecules in the perpendicular meridian, and will therefore receive less scattered light. Moreover, since Latimer's recent studies [21] suggest that algal chloroplasts are remarkably effective scatterers, differential scattering cannot be lightly dismissed as too small an effect.

(ii) *Photoreceptor orientation:* This is the most attractive possibility, since the dichroic ratios of most dyes [20] are plainly large enough to explain the polarotropic response if these molecules were but oriented properly in the cell. Since the zygote looks and acts as though it were radially symmetrical, the only reference point for photoreceptor orientation is the cell surface. Hence these molecules, if they are oriented at all, must either tend to have their axes of maximum absorption arranged parallel to or perpendicular to the nearby cell surface. Examination of Fig. 6 shows that a parallel orientation is the requisite one. Acting together with the by-passing effect, it would cause the photoreceptor molecules in the germinating region to absorb the smallest fraction of the light passing through.

The one structure in which the arrangement of photoreceptor molecules is definitely known is the vertebrate rod. It is notable that this arrangement is analogous to that postulated above for the *Fucaceae* zygote. For the axes of maximum absorption in the rod lie in planes perpendicular to the rod and anisotropically within these planes [9, 28]; hence they lie periclinally, i.e. parallel to the nearby membranes [10, 30].

The only report of polarotropism, other than in the *Fucaceae* zygote, is that of Castle in the *Phycomyces* sporangiophore [5]. It is notable that this finding is most readily rationalized by invoking an arrangement of dichroic photoreceptors again analogous to that postulated for the *Fucaceae* zygote. Contrary to Castle's claim, differential reflection cannot explain the observation [17], while an alignment of photoreceptors in the direction of greatest wall strain can. In the case of the spherical *Fuceacae* zygotes this is simply the postulated periclinal one; in the case of the cylindrical sporangiophore, it is further restricted, being both periclinal and perpendicular to the cell's long axis [6].

Finally, it may be noted that the close-packed tubular membranes of the arthropod ommatidium are believed to define the region in which the photoreceptor molecules lie, and are so arranged that a periclinal arrangement of these photoreceptors could explain the capacity of the arthropod eye to detect the plane of vibration of light [11, 23, 35].

SUMMARY

The following picture is drawn from experiments on two members of the Fucaceae, *Fucus furcatus* and *Pelvetia fastigiata:*

1. In their "polarotropic" response to unidirectional illumination with plane polarized visible light, the zygotes tend to germinate in the plane of vibration, and "subequatorially" (from 90° to 135° away from the source). (Fig. 1.) Up to half the embryos so produced may be bipolar forms.

2. The tropistic response to similar unpolarized light is dual. Under some partially defined conditions it is subequatorial; under others, directly away from the source.

3. The polarotropic response and the subequatorial response to unpolarized light fade out over the same intensity range (Fig. 4).

4. The polarotropic action spectra (Fig. 3) belong to the phototropic group of spectra as found with other organisms (Table VI).

5. It is concluded that in all three tropistic responses to light, growth tends to occur where certain photoreceptor molecules absorb the least light.

6. It is suggested that under unpolarized illumination the subequatorial

and peripheral photoreceptors absorb least light primarily because they are by-passed by the cell's focusing action (Fig. 5), while under polarized illumination the subequatorial photoreceptors in the vibration plane absorb least light because they are periclinally oriented (Fig. 6).

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