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Action spectrum for the blue-light-dependent morphogenesis of hair whorls in *Acetabularia mediterranea*

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Abstract. In young *Acetabularia mediterranea* Lamouroux (=*A. acetabulum* (L.) Silva) the formation of the lateral hair whorls can be induced by a short pulse of blue light after continuous red preillumination. In this paper we describe the experimental conditions for optimum response and the properties of the action spectrum. The probit of the cells which eventually form hair whorls is linearly correlated to the logarithm of the incident quanta of blue light. Parallel fluence-response curves for all wavelengths indicate the involvement of only one photoreceptor pigment. The action spectrum shows no effectiveness of wavelengths above 520 nm, a high action peak at 470 nm and two lower ones at 425 and 370 nm, and is in accordance with those of cryptochrome-like photoreceptors.

Key words: *Acetabularia* – Action spectrum – Blue light – Hair whorls (*Acetabularia*) – Photomorphogenesis.

Introduction

The siphonaceous green alga *Acetabularia mediterranea* is a useful model system for studies of photomorphogenesis (Clauss 1968, 1970, 1973; Schmid 1984). Although unicellular, its vegetative development is characterized by the formation of well-defined differentiations at the growing apex of the cell. These are the lateral hair whorls which are produced in regular intervals, and the cap which originates at the end of the vegetative growth phase (Hämmerling 1934). The formation of these differentiations requires the action of blue light (Clauss 1963, 1968; Richter 1962). Under continuous red light, i.e. in the absence of blue light, the growth rate of the cell declines to almost zero within one to two weeks (Clauss 1968). Hairs or caps develop only very occasionally in red light.

Acetabularia mediterranea is highly sensitive to blue irradiation which, when added to continuous red light for only a few seconds once a day, markedly enhances the growth rate and allows the formation of hairs and caps (Clauss 1968). We have taken advantage of the sensitivity of this organism to establish an experimental procedure which allows the quantitative evaluation of the morphogenetic response to a single pulse of blue light. In this publication we describe the conditions required for optimum response and present a detailed action spectrum.

Material and methods

Light sources. Under white light the dishes containing the cells were irradiated laterally by fluorescent tubes (65W/15; Osram, München, FRG) at an intensity of 2500 lx in light: dark cycles of 10:14 h.

As a standard red-light source we used a combination of red fluorescent lamps (TL 15/40 W; Philips, Eindhoven, The Netherlands) and red plexiglass (Nr. 501; Röhm and Haas, Darmstadt, FRG) as described by Mohr et al. (1964), with a standard photon fluence rate of $1.6 \cdot 10^{-5}$ mol·m^{-2}·s^{-1}. The broad-band standard blue-light source, taken for some of the experiments, consisted of blue fluorescent tubes (TL18/40W; Philips) and an additional filter ("blaues Signalglas", 2 mm; Schott, Mainz, FRG). This light source emitted a small portion of far-red light, which is ineffective in hair-whorl formation (data not shown).

Monochromatic irradiation for the action spectroscopy was produced as described by Mohr and Schoser (1959). The light was supplied from Leitz projectors equipped with Xenon high-pressure lamps (XBO 450 W; Osram). The latter are more useful in the blue-green and UV spectral region than tungsten bulbs (Raschke 1967). The light was passed through interference filters of different types: UV-IL, AL, DIL, and DAL (Schott). Except for the UV-A, the light was prefiltered through a heat-absorbing glass (K 61, 2 mm; Schott).

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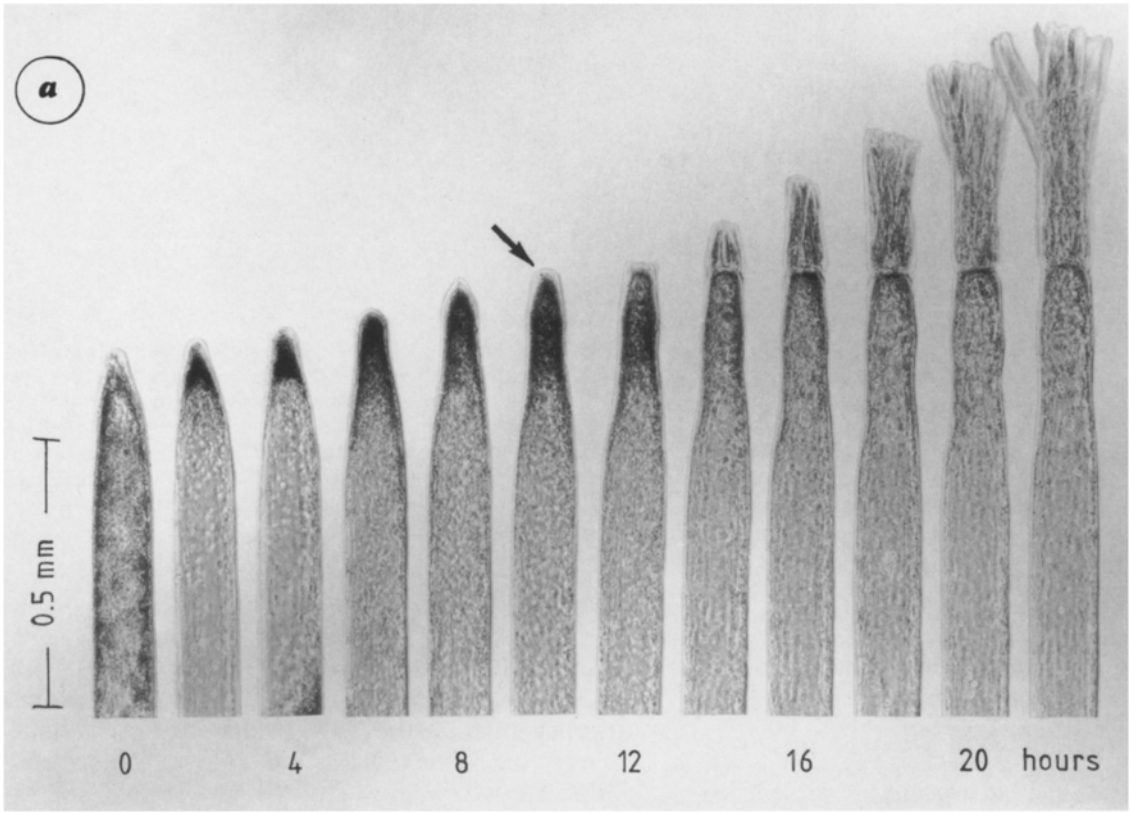

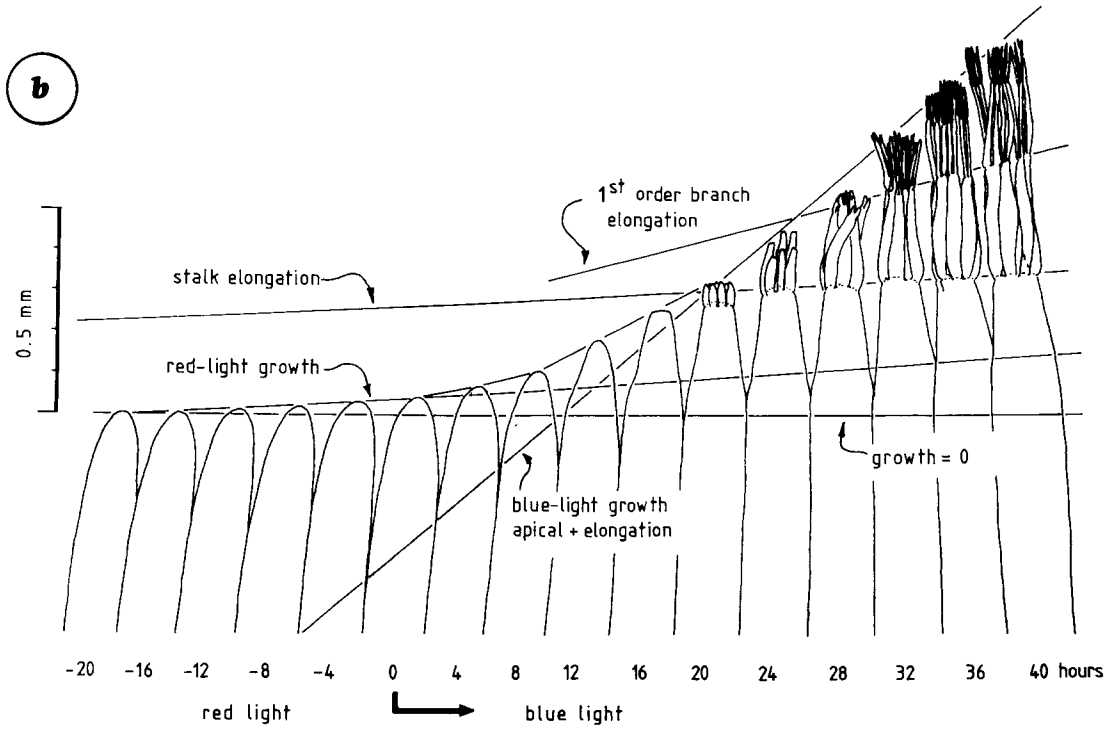

Fig. 1a, b. Morphology of the stalk apex of *Acetabularia* in continuous blue light after 7 d of red preirradiation. **a** shows a series of photographs taken at 2-h intervals. The *arrow* points to the flattening of the tip which is the first visible sign of the hair-whorl formation. The line drawing in **b** gives additional information about growth rates under red light and after blue-light induction. The term "elongation" means growth without synthesis of cell wall, while "apical" growth is caused by the formation of new wall material at the very apex. The line "growth = 0" indicates a growth rate of zero. In both figures the start of blue irradiation is defined as the time "0". Points of time before the onset of blue light (red light) are, therefore, negative

Different photon fluence rates were obtained either by variation of the distance to the light source or by the insertion of neural-density filters (Schott). The respective fluence rates were adjusted using a thermopile (Kipp and Zonen, Delft, The Netherlands).

Culture conditions. The temperature was $21 \pm 1°$ C throughout. The standard procedure for raising the algal material was as follows: Stock cultures of young germlings of *Acetabularia mediterranea* Lamouroux (= *A. acetabulum* (L.) Silva) were kept in darkness and regularly irradiated every four weeks for 2 d with white light (Hämmerling 1944). Under these conditions they can be stored for several years. The culture medium was "Erd-Schreiber" medium (Beth 1953) or artificial seawater (Schweiger et al. 1977). Cells for the experiments were taken from the stock cultures and exposed to white light in culture dishes (diameter 10 cm, height 6 cm). Eleven days later they were collected and transferred into plastic Petri dishes (diameter 5.5 cm) containing 10 ml of medium. The density of the cells was chosen to be 100–150 cells per dish. Upon a further 3 d in white light the Petri dishes were placed under the red-light source for 7 d. At the beginning of the blue irradiation the cells were no longer than 3 mm. On the sixth day in red light the medium was changed once again. After this red-light pretreatment the cells were given the inductive blue irradiation (the blue-light conditions are indicated in the legends to the figures) and were then returned to red light. The photon fluence rate of the red light after the induction was $2.1 \cdot 10$ mol $\cdot m^{-2} \cdot s^{-1}$. Twenty-six to 28 h later the percentage of cells with new hair whorls was counted under a stereo microscope. The new whorls were distinguishable by their apical position from those formed earlier under the preculture in white light.

Corrections and precautions. As a small number of the cells also formed hairs under red-light conditions, all of the values shown are corrected for this blue-light-independent hair formation.

The number of cells which were able to develop new hairs after a saturating inductive blue-light pulse varied from experiment to experiment under identical conditions even when the same culture was taken. Therefore, we regularly determined this percentage as a control. With regard to the fluence-response curves, these controls were used as the 100% basis to recalculate the other data of the same experimental set. Furthermore, the fluence-response relations of different cultures showed different thresholds and slopes. Thus we used only one culture for action spectroscopy.

Results

Growth characteristics and morphology of the apex before and after induction. In red light the stalk elongation rate slowed down, as has already been reported by Clauss (1968). After a switch to blue light or upon a short blue-light pulse the growth rate began to accelerate again (Fig. 1b; Figs. 1a and b depict the process in continuous blue light). Within 2–4 h the elongation rate increased to 0.5–1.5 $\mu m \cdot h^{-1}$, i.e. about the 10- to 15-fold the rate at the end of the red-light irradiation.

Within the first 2 h after the beginning of the blue irradiation we observed, at the very apex of the stalk, the accumulation of clear hyaline cytoplasmic material which was not present or was

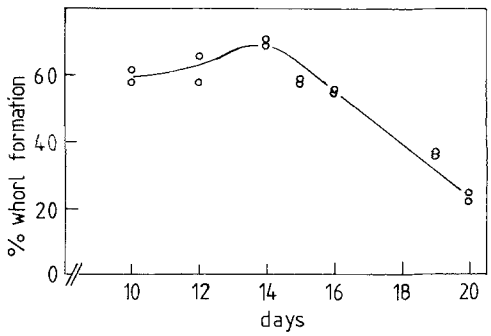

Fig. 2. Dependency of the blue-light response of hair-whorl formation on the duration of the preculture in white light. *Acetabularia* germlings from the stock cultures were grown for different periods in white light. This was followed by one week of irradiation by the standard red-light source. After the induction by a saturating blue-light pulse of 12.5 min at 1.1 $W \cdot m^{-2}$ and a further day in red light, the number of cells with new hairs was counted

strongly reduced in red light (Fig. 1a). This process was accompanied by the initiation of chloroplast condensation further down the stalk. After 10–16 h this dense chloroplast zone disappeared and the tip began to flatten (Fig. 1a: arrow). At the margins of the flattening area little nipples were formed (Fig. 1a) which grew out as single hairs. The hyaline plasmatic cap was distributed and transposed into the tips of the growing hairs. Later on, the hairs began to branch simultaneously. When the formation of the hairs was completed, the centre of the stalk apex formed a new growing tip. The continuation of the growth of the new cell apex caused the hairs to fold down into their final lateral position.

Before the acceleration of growth there was a lag phase of 1–2 h which appeared to be connected with the formation of the hyaline cytoplasmic region. We conclude from the behaviour of this region and the different growth rates (Fig. 1b) that growth in *Acetabularia* is, like that in higher plants, the result of two different components: i) an active component which is connected with the formation of new wall material and is restricted to the very tip of the cell; ii) a "passive" component which gives rise to cell elongation by stretching of the cell wall. We found the highest growth rates when the hyaline apical region was present (Fig. 1b, "blue light growth, apical + elongation"). Therefore, the active apical growth appeared to be a consequence of this hyaline cytoplasmatic portion. Since under red-light conditions this region was lacking, only "elongation" growth should occur, and in fact the growth rate found in red light was very similar to that of the stalk after blue-light induction, when there was no further "apical"

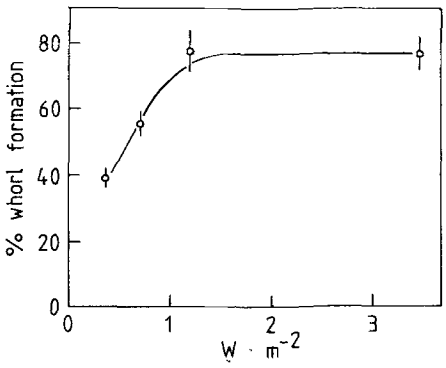

Fig. 3. Influence of the fluence rate of the red preirradiation on the response of *Acetabularia* to blue light. Cells from the stock cultures were cultivated for 12 d in white light. This was followed by one week of red light of different fluence rate. After a saturating blue-light pulse (1 h at 6.3 $W \cdot m^{-2}$) all of the cells were kept for a further 1 d under standard red-light conditions, and the number of cells with new whorls was then counted

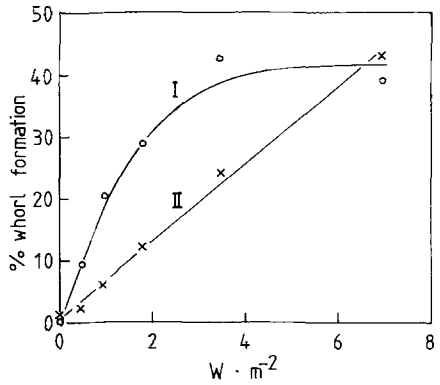

Fig. 5. Effect of the fluence rate of the red light which follows the induction by blue light on the formation of hair whorls by different cultures (*I, II*) of *Acetabularia*. After 12 d in white light the cells were irradiated for 7 d with red light. Hair formation then was induced by 10 min of standard blue light (4.8 $W \cdot m^{-2}$) after which red light of different fluence rates was given. After 1 d the percentage of cells with new hair whorls was determined

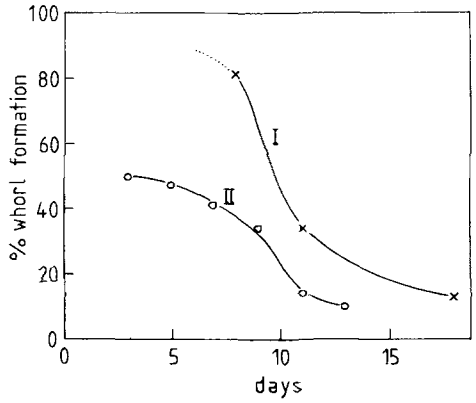

Fig. 4. Influence of the duration of the red-light preirradiation on the ability of *Acetabularia* to develop a hair whorl after induction by blue light. The results of two experiments with different cultures (*I, II*) are shown. Germlings from the stock cultures were cultivated for 12 d in white light. This was followed by irradiation with red light (3.5 $W \cdot m^{-2}$) of various durations. Hair formation was induced by 1 h of standard blue light (6 $W \cdot m^{-2}$). After a further day in red light the percentage of cells with new hair whorls was determined

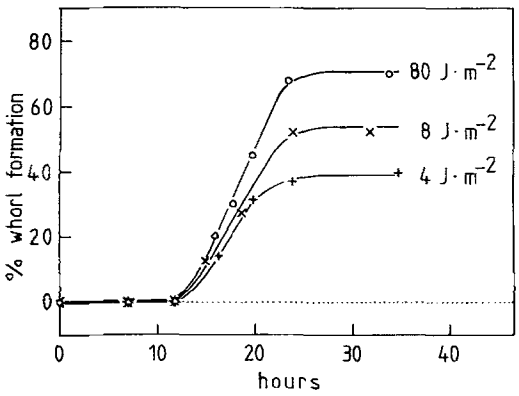

Fig. 6. Time course of the formation of hair whorls at the cell apex of *Acetabularia* after induction by blue light of different fluences. After 12 d of culture in white light the cells were irradiated for 7 d with red light. The formation of hair whorls was induced by 10 min of blue light at the fluences indicated in the figure. The percentage of cells with new hair whorls was evaluated during further irradiation with red light

growth of the cell's main axis, i.e. when the hyaline region had divided and was active in forming the hairs (compare "red-light growth" and "stalk elongation" in Fig. 1b). The increase in stalk length at this time must only be the result of elongation.

Preconditions for optimum response. A saturating blue-light pulse could not induce all of the cells to form hair whorls. The inducibility was very different in the cultures used. Maximum formation of new whorls varied from 20% to somewhat above 90%. Thus for the experiments, only cultures which showed at least a 70% response were taken. Apart from this, the ability to form whorls after induction by blue light was dependent on a number of other different factors as shown below. Accordingly, in the later standard procedure the conditions were chosen to give optimum response.

During preculture in white light the cells had firstly to become capable of forming hairs, and it was only after about 10 d that most of the cells finally produced at least one hair whorl. At this stage, it was possible to induce the formation of new hair whorls after a further week in red light. An optimum number of inducible cells, however,

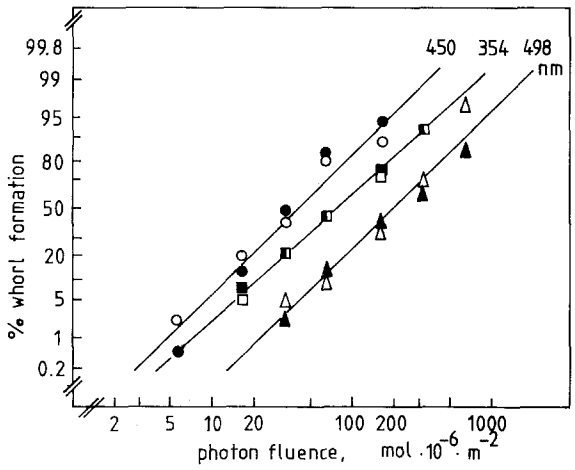

Fig. 7. Photon fluence-response curves of light-induced hair-whorl formation and the demonstration of reciprocity for three different wavelengths. For the light treatments the standard procedure was followed. Hair-whorl formation was induced with monochromatic light of three different wavelengths. For each of the wavelengths two different fluence rates were applied: a high rate ($1.68 \cdot 10^{-6}$ mol photons$\cdot m^{-2} \cdot s^{-1}$) and a rate which was only one-sixth (498 and 450 nm) or one-third (354 nm). (The irradiation times were increased six- and threefold, respectively.) *Open symbols* are the values obtained with the high fluence rates. The values are corrected by a red-light control (0%) and a control which had been induced by a saturating blue-light pulse of 450 nm (100%). The probit of the percentage of hair-whorl formation is plotted versus the logarithm of the photon fluence

was obtained when the preculture in white light was about 14 d (Fig. 2). Thereafter the responsiveness slowly decreased again with increasing age.

The number of inducible cells depended strongly on the fluence rate of the red preirradiation (Fig. 3). Only fluence rates above 1.5 W$\cdot m^{-2}$ were saturating and gave the best response to the subsequent blue light.

When the duration of the red preirradiation exceeded 7 d, the responsiveness to the inductive blue light drastically decreased (Fig. 4). The blue-light effect was better with shorter red-light pretreatments. (When the red irradiations were shorter than 3 d the evaluation was hindered since new hair whorls were no longer unequivocally distinguishable from those formed or initiated shortly before the beginning of red light. We choose a red-light duration of 7 d in the following experiments as the standard.) The most critical condition for a high response was the fluence rate of the red irradiation after the inductive blue-light pulse. Different cultures also had different requirements (Fig. 5). Some of them were saturated with 3–4 W$\cdot m^{-2}$ of red light while in others no saturation could be found even at 7 W$\cdot m^{-2}$. One of the cultures had only a very low requirement for this post-inductive red irradiance and at least 20% of the cells were capable of forming hairs even in complete darkness (data not shown).

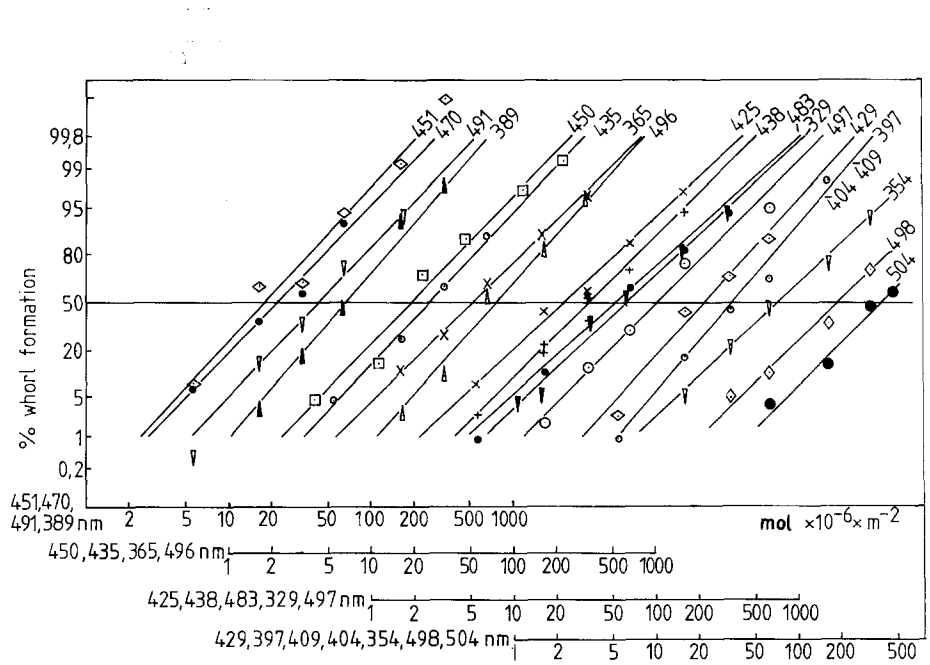

Fig. 8. Photon fluence-response curves of the light-induced hair-whorl formation for different wavelengths. For the light treatments the standard procedure was followed. The wavelengths used for induction are indicated at the respective plots. The monochromatic light sources were set to equal fluence rates of $5.62 \cdot 10^{-7}$ mol photons$\cdot m^{-2} \cdot s^{-1}$. The corrected (see Fig. 7) percentage of hair-whorl formation is plotted versus the logarithm of the photon fluence with different abscissae for the different wavelengths

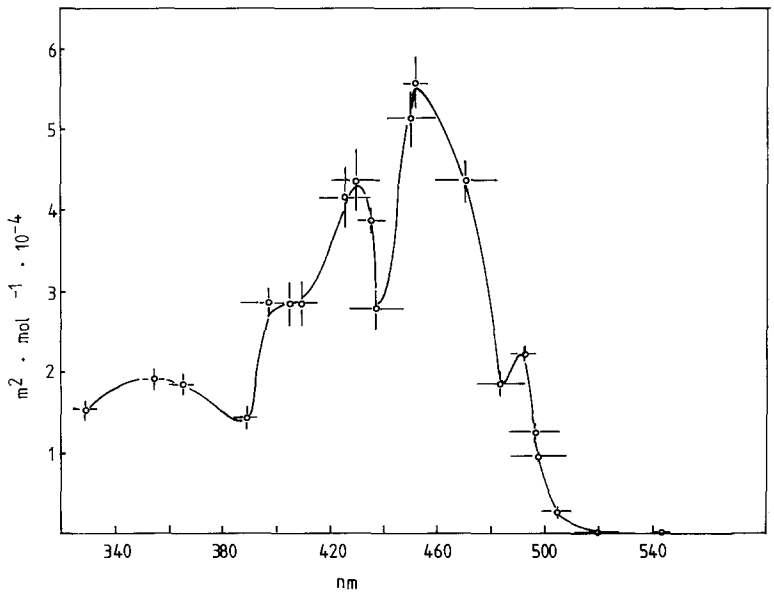

Fig. 9. Action spectrum of light-induced hair-whorl formation in *Acetabularia*. The reciprocal photon fluence required to induce 50% of the cells to form a hair whorl (see **Fig. 8**) is plotted versus the wavelength. *Vertical bars* indicate the deviations which result from the intersects on the 50% line in **Fig. 8**, using upper and lower maximal deviations of the linear regressions of the fluence-response curves. *Horizontal bars* give the half band-widths of the interference filters

The response to blue light. In all experiments, described below, the standard procedure was applied as indicated in *Material and methods.*

Blue light given after the red preirradiation induced the cells to synchronous hair-whorl formation (Fig. 6). The number of responding cells depended on the fluence of blue light, but the time course of hair formation was unaffected (Fig. 6). The percentage of cells with new hairs plotted versus the logarithm of the photon fluence was linear on a probit scale (Figs. 7, 8). Within the tested range the response to blue light followed the law of reciprocity. This was shown for three different wavelengths (Fig. 7). Reciprocity was also found with broad-band blue light (standard blue light source). We believe, therefore, that this holds for the whole range of effective wavelengths.

The linear regressions of the fluence-response relations for the various wavelengths were parallel within the limits of the error (Fig. 8). Plots of the slopes of the lines versus the wavelength were randomly distributed around a line parallel to the wavelength axis and did not show any spectral dependency. The action spectrum shown (Fig. 9) was calculated for a responsiveness of 50%. No effectiveness was found for wavelengths above 520 nm. Major maxima were prominent at 450 and 430 nm with a minor peak in the UV A region at 350 nm.

Discussion

It is evident from earlier investigations (Clauss 1968) that, under red light, morphogenesis in *Acetabularia mediterranea,* i.e. the formation of hairs and the cap, occurs only accidentally. Furthermore, growth becomes strongly retarded. Subsequent blue light reaccelerates growth and restores the capability for morphogenesis. The absence of growth in prolonged red light is difficult to interpret: the lack of morphogenetic events may be the consequence of the growth reduction or morphogenesis itself may be under the control of light. Two arguments are in favour of the latter: i) When the cells are irradiated with blue light after a prolonged red-light pretreatment they form new hair whorls with a high synchroneity between the 10th and the 20th hour (Fig. 6). This was observed with all cultures, although the time which elapsed between the formation of two successive whorls varied between 1 and 5 d in the different progenies. This indicates that the usual cycle of formation of hair whorls is interrupted at a defined step which requires blue light for completion. ii) In the related species *Acetabularia calyculus* the growth rates in red and blue light are similar and only the formation of hairs and caps is under blue-light control (Clauss 1973).

The reduction of the percentage of hair-whorl formation when low fluence rates of red light are used either before or after the blue-light pulse may be due either to a limited supply of photosynthetic products or to the action of phytochrome. It is satisfactory to explain the results exclusively on the basis of the deficiency of photosynthetic products. Of course, the active growth of the cell's apex and the formation of hair whorls requires the presence of carbohydrates and energy. Therefore, the role of the red irradiation after blue light in order

to supply photosynthate is evident, although different cultures seem to differ in their requirement for this irradiation (Fig. 5). The role of the red pretreatment may also be interpreted in the same sense: It has been shown for *Acetabularia mediterranea* that under prolonged red irradiation an excess of storage products (starch) is accumulated and that these can be mobilized by subsequent blue light (Clauss 1972; Schmid and Clauss 1977). As reserve carbohydrates are photosynthetic products, their amount is dependent on the red-light fluence rate. Therefore, if the latter is low, this may limit the blue-light-induced growth. For these reasons at least one of the effects of red light is certainly to sustain photosynthesis, but additional influences via phytochrome cannot be excluded. If there is an effect of phytochrome, i) the dependency on the fluence rate of red light would point to a high-irradiance phenomenon and ii) it must be synergistic with blue light at least with respect to the formation of the hairs. In this case, continuous far-red light should be more effective for the high-irradiance response. Bichromatic irradiation could be a possible test.

After long red preirradiations the ability to develop hairs drops dramatically (Fig. 4). This may be associated with the fact that essential metabolic activities, such as photosynthesis (Schael and Clauss 1968; Clauss 1970, 1972) or respiration (data not shown) decrease under red-light conditions. The reactivation of photosynthesis and respiration by blue light is slow compared with the induction of growth and morphogenesis and thus these former activities may become limiting when the preirradiation by red light exceeds a critical period.

We would like to stress the point that the ability to respond to induction by blue light varied strongly in the different cultures tested (see for example Figs. 4, 5) although the response proved to be uniform and reproducible in the definite progenies. The differences may have a variety of causes not necessarily connected to the blue-light response itself. The requirement for red light may also limit responsiveness (Figs. 4, 5). The ability of the different progenies to respond to blue light are apparently inherited (data not shown). This offers the possibility of isolating strains of *Acetabularia mediterranea* which differ in their morphogenetic response to blue light, and thus may allow a more detailed insight into the response to blue light, as well as into the mechanism of morphogenesis of hairs, to be obtained.

Since the law of reciprocity was found to be valid for the response of hair formation (Fig. 7), the amount of absorbed photons determines whether a cell responds or not. Furthermore, the fact that the fluence-response curves are parallel on the logarithmic fluence scale (Figs. 7, 8) indicates the involvement of only one photoreceptor in the response.

An action spectrum – with some restrictions (Schäfer and Fukshansky 1984) – theoretically represents the absorption spectrum of the photoreceptor pigment for the response in question. The action spectrum for light-induced hair formation in *Acetabularia mediterranea* (Fig. 9) shows strong similarities to those in other plants, fungi, and animals (Curry and Gruen 1959; Delbrück and Shropshire 1960; Curry and Thimann 1961; Rau 1967; Seitz 1967; Zurzycki 1967; De Fabo et al. 1976; Klemm and Ninnemann 1976; Mizukami and Wada 1981) which are characteristic of photoreceptors called "cryptochrome" (Senger 1984). However, the deep incision at 438 nm is unusual. The discussion about the chemical nature of the photoreceptors in chryptochrome-like action spectra is still controversial, favouring either flavins or carotenoids as possible candidates (for a detailed compilation of the arguments, see De Fabo 1980). Although the action spectrum cannot solve this question, it serves to classify the effect as typically blue-light-dependent. On the other hand, we must take into account that the term "cryptochrome" puts together a rather heterologous class of photoreceptors.

Recently, the presence of light-induced absorption changes (LIACs) in plasma-membrane preparations of *Acetabularia mediterranea* have been shown (Caubergs et al. 1984). These LIACs are reported to be due to the reduction of a *b*-type cytochrome by a flavin photoreceptor (Muñoz and Butler 1975). The latter is often proposed to be the blue-light receptor in vivo. The photoreceptor system, responsible for the induction of growth and morphogenesis in *Acetabularia,* might have the characteristics of a LIAC. For a proof, however, it is necessary to demonstrate a connection between the LIAC and the physiological response.

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