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Investigations on the Phototactic Orientation of *Anabaena variabilis*

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Abstract. Phototaxis of the blue-green alga *Anabaena variabilis* was studied using both population method and observation of single trichomes by microscope. The trichomes react positively at low and negatively at high illuminance. The inversion point lies at about 1000 lx. The action spectrum of positive phototaxis indicates that the photosynthetic pigments chlorophyll a, C-phycocyanin and allo-phycocyanin are involved in the absorption of the active light. The same range of wavelengths is active in negative phototaxis, but in addition, wavelengths between 500 and 560 nm and between 700 and 750 nm are also effective. Obviously pigments of unknown chemical nature are sharing in light absorption. Two alternatives are discussed. Since inhibitors of photosynthesis such as DCMU and DBMIB do not affect phototactic orientation, a direct coupling of phototaxis with photosynthesis can be excluded.

Key words: Movement – Phototaxis – Action spectrum – Blue-green algae – Cyanophyceae – *Anabaena variabilis* – Inhibitors.

In blue-green algae of the familiy Oscillatoriaceae which under diffuse light display an alternating backward and forward movement without preferring any direction, phototaxis is brought about by a change of the autonomous rhythm of reversal (Drews, 1957, 1959; Nultsch, 1961, 1975). At the onset of unilateral illumination the trichomes do not orient themselves to the direction of the incident light beam. However, in individuals which are in a position more or less parallel to the light beam the movement toward the light source is prolonged while the movement away from it is shortened. With negative reactions the opposite is true. In trichomes oriented perpendicularly to the light beam no phototactic effect can be observed.

In blue-green algae of the family Nostocaceae, however, such as *Anabaena* and *Cylindrospermum*, phototactic orientation is the result of an active steering (Drews, 1957, 1959), the mechanism of which is unknown. Contrary to *Phormidium autumnale* and *Phormidium uncinatum* (Nultsch, 1962), *Anabaena* and *Cylindrospermum* display phototactic reactions even in red light (Drews, 1959). This has been confirmed recently by Tyagi (1976), who measured a rough action spectrum of *Cylindrospermum alatosporum* in the visible range.

Thus, in both families phototaxis seems to be brought about by different mechanisms. Therefore the phototactic behaviour of *Anabaena variabilis* has been investigated in detail.

Material and Methods

The *Anabaena varibilis* strain B 1403-10 of the culture collection of the Pflanzenphysiologisches Institut Göttingen which has been used for the investigation of photokinesis (Nultsch and Hellmann, 1972) has completely lost its ability of phototactic orientation. Therefore the strain B 377 of *Anabaena variabilis* (Kütz.) obtained from the culture collection of algae at Indiana University was used, which moves relatively fast and displays strong phototactic reactions.

The algae were grown at 21° C under continuous fluorescent light (400 lx) in petri dishes on membrane filters (type 11307, Sartorius, Göttingen) which were put on glass wool soaked with nutrient medium. This contained per liter: 0.2 g KNO_3, 0.02 g $KH_2PO_4 \cdot 3H_2O$ and 0.02 g $MgSO_4 \cdot 7H_2O$. 0.5 ml trace element solution (A–Z, Hoagland) and 50 ml earth decoct were added. The medium was sterilized at 1 bar for 30 min.

The cultures were used for the experiments 5 days after inoculation. Petri dishes filled with tap water agar (0.3%) were

Abbreviations. DCMU = 3-(3,4-dichlorophenyl)-1,1-dimethylurea, DBMIB = Dibromothymoquinone (2,5-dibromo-3-methyl-6-isopropyl-*p*-benzoquinone)

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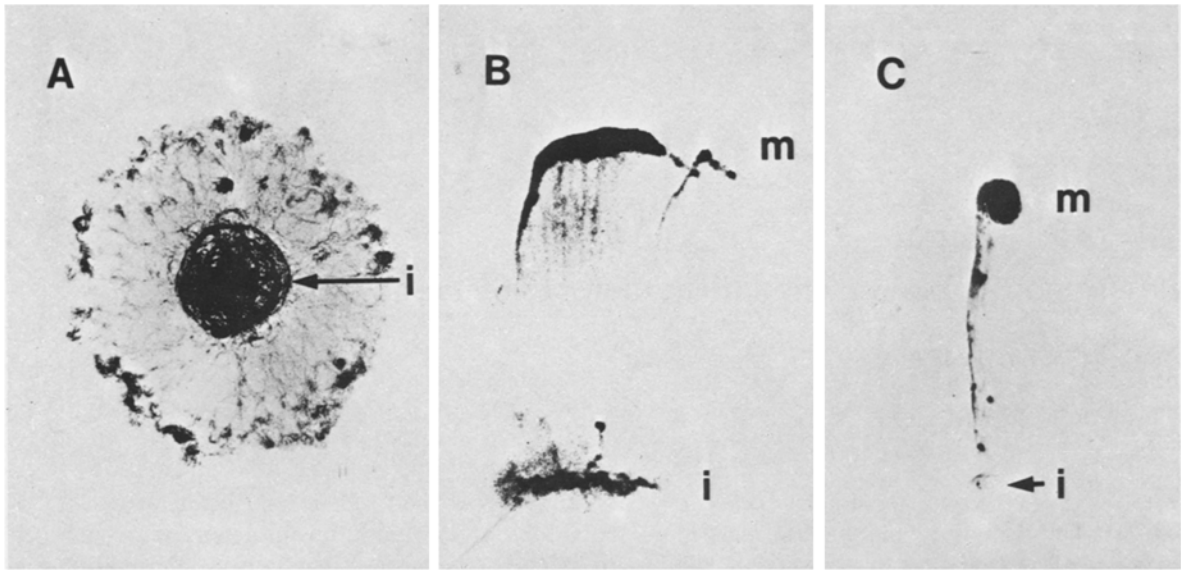

Fig. 1 A—C. Spreading patterns of *Anabaena* on an agar plate: **A** circular spreading area, **B** phototactic migration toward the light source, **C** all trichomes form a migrating mass, so that no organisms are left at the inoculation spot. *m* migrating mass; *i* inoculation spot (magn. 2×)

inoculated in the centre with about 20 mg algal mass (fresh weight) and then exposed to unilateral white light or monochromatic irradiation for 4 days. The inoculation spot had a diameter of 0.5 cm. For white light illumination projectors (Leitz, Prado) with quartz iodide lamps (Osram 24 V, 250 W) were used. Different illuminances were obtained by inserting neutral density filters in order to avoid changes of the color temperature. Monochromatic light was achieved with interference filters (Schott & Gen.) in the visible range and with Xenon arc projectors (Schöffel Instr., type 102; lamp: Osram XBO 900 W) as light sources and grating monochromators (Schöffel Instr., GM 250) in the UV. The half band width of the interference filters varied between 10 and 14 nm. The energy was measured by a thermopile (Kipp & Zonen) coupled with a microvoltmeter (Keithley). The temperature during the experiments was 20° C.

An individual cell method as well as a population method (Nultsch, 1975) were used to measure phototactic reactions. In the first case the behaviour of single trichomes under unilateral illumination was studied by tracing their tracks with the aid of Abbe's apparatus. In the population method the movement of the cell masses toward the light source or away from it was evaluated. If the radiation is phototactically inactive, the trichomes spread more or less circularly away from the inoculation spot on the agar plate (Fig. 1 A). A slight phototactic effect is indicated by shifting the speading area toward the light source or away from it, so that it becomes excentric. In this case the difference between the distances from the inoculation spot to the margins of the spreading area can be used as a measure of the phototactic effect. If the phototactic effectiveness is strong, the algae move exclusively toward the light source in positive and away from it in negative reactions (Fig. 1 B). In this case the distance between the inoculation spot and the front of the migrating algae was used as a measure. Sometimes all the algae move simultaneously with the same speed, forming a coherent mass (Fig. 1 C).

However, it must be taken into account, that the distance traversed in a given time does not exclusively depend on the directness of movement as a result of the phototactic effectiveness of the unilateral irradiation, but also on the speed of movement, which in turn can be influenced by the stimulus light when it is photokinetically active (Nultsch, 1975). Since in most of the experiments all the trichomes moved either toward the light source or away from it, the photokinetic correction of the reaction values as suggested by Nultsch (1961) for *Phormidium* was not applicable. Moreover, the phototactically active wavelengths are also photokinetically effective, so that the photokinetic effect of the stimulus light could not be eliminated by a simultaneous background illumination, because the phototactic effect would be nullified this way. However, the photokinetic correction of the phototactic reaction values might not be so important in this case, since rough action spectra measured at different irradiances have shown that photokinesis is saturated at the irradiances used in the phototactic experiments. In this respect the strain B 377 (Indiana University) differs from the B 1403-10 strain (Göttingen) investigated by Nultsch and Hellmann (1972).

Polarographic measurements of the photosynthetic O_2-production were performed with an oxigraph (Gilson K-IC). The samples (1.8 ml) were irradiated with a projector (Leitz Prado, lamp: Osram 24 V, 250 W). A cut off filter (OG 590, Schott & Gen.) was inserted to eliminate the effect of blue light on respiration (cf. Kowallik, 1969). The light beam was collected by a focussing lens ($f = 5.5$ cm) so that an irradiance of more than 5000 Wm^{-2} could be obtained. Since irradiances higher than 500 Wm^{-2} caused an increase of O_2-consumption in the following dark period, measurements were performed with non saturating orange light (125 Wm^{-2}; lamp voltage was reduced to 7.8 V). The absorption spectrum was determined with a Shimadzu MPS 5000 recording photometer. 0.33 g algal mass (fresh weight) was suspended in 2.5 ml aqua dest. and measured in 1 × 1 cm cuvettes against aqua dest. as reference.

Results

Phototactic Behaviour of Single Trichomes. The phototactic behaviour of more than hundred trichomes under unilateral illumination has been studied tracing their tracks. A few of the drawings are shown in Fig. 2 A – F as examples for typical modes of behaviour, which are schematically represented in Fig. 2 G – K. As already reported by Drews (1959), under unilateral illumi-

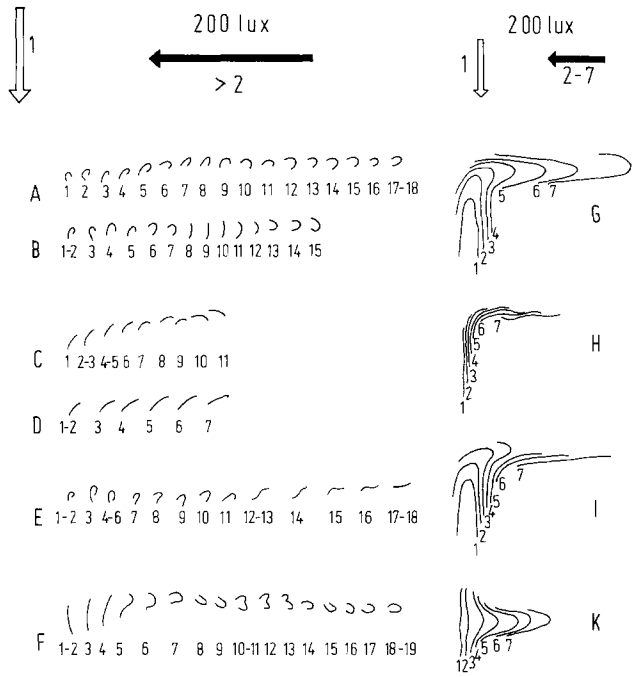

Fig. 2. Change of movement direction of *Anabaena* trichomes at 200 lx. *Light arrow:* initial light direction; *dark arrow:* new light direction. The number 1 denotes the initial position of the trichome, the following numbers the positions in 1 min intervals after changing the light direction. Each drawing is shifted to the right hand for better resolution. Two or more numbers at the same trichome indicate that the positions have not changed during the last minute(s). *A*, *B* behaviour of U formed trichomes. *C*, *D* behaviour of straight trichomes. *E* U formed trichome becoming straight after change of light direction. *F* Straight trichome becoming U formed after change of light direction. *G–K* Schematic representations of the behaviour types shown in *A–F*

nation the filaments of *Anabaena* form often a U like figure with its axis of symmetry oriented parallel to the light beam. The bending points toward the light source in case of positive reaction. If the light direction is changed, e.g. at a right angle to the original direction, the tip of the bend begins to turn until the U is again directed to the light source (Fig. 2A, B, G). However, even approximately straight filaments orient themselves more or less parallel to the light direction. In this case their tips turn toward the light source, after the light direction has been changed, until the whole filament is parallel to the light beam again (Fig. 2C, D, H). Sometimes it happens that straight trichomes which are oriented perpendicularly to the light beam, after the light direction has been changed, begin to bend approximately in the middle of the filament becoming U formed this way (Fig. 2F, K). On the other hand, U formed trichomes can become straight if illuminated from the side (Fig. 2E, I). In case of negative reactions the trichomes display the same behaviour, but in the opposite sense. Thus, the bending of the trichomes is an active orientation to the light direction as reported by Drews (1959).

White Light Illuminance-Response Curve. The illuminance-response curve measured with the population method in white light is shown in Fig. 3. At low illuminances between 1 and 1000 lx the trichomes respond positively, i.e. they move toward the light source. The optimum of positive phototaxis lies around 200 lx. With further increasing illuminance the positive response becomes less pronounced, and at about 1000 lx the inversion point is reached, at which no clear phototactic orientation can be observed. Above 1000 lx the algae react negatively.

Action Spectrum of Phototaxis. In order to obtain action spectra of positive and negative phototaxis irradiance-response curves at various wavelengths between 350 and 732 nm were measured. Photon fluence rates between $1.12 \cdot 10^{-11}$ and $5.6 \cdot 10^{-8}$ mol cm^{-2} s^{-1} were used between 513 and 732 nm. Between 350 and 412 nm only $1.12 \cdot 10^{-8}$ mol cm^{-2} s^{-1} and between 420 and 513 nm $2.8 \cdot 10^{-8}$ mol cm^{-2} s^{-1} could be produced as maximal photon fluence rates with the light sources available.

At most wavelengths which are phototactically effective the organisms display positive responses at lower and negative responses at higher photon fluence rates. As shown in Fig. 4, the irradiance-response curves obtained for positive phototaxis are optimum curves which do not reach a saturation level. The optimum levels are different, but the optimal photon fluence rates are of the same order of magnitude (around $5 \cdot 10^{-10}$ mol cm^{-2} s^{-1}). Even the inversion point fluence rates at which the positive reaction becomes negative are of the same order of magnitude (between 10^{-9} and 10^{-8} mol cm^{-2} s^{-1}). Within this range the inversion point seems to be shifted to higher photon fluence rates the more the stronger the phototactic activity of the wavelength is. This, however, might not be significant, since the standard deviation of the individual points of the irradiance-response curves is about 10–15%. From the shape of these curves it may be concluded that more than one photoprocess is involved in perception of the phototactic stimulus. At 542 nm no reactions are found between $1.12 \cdot 10^{-11}$ and $5.6 \cdot 10^{-10}$ mol cm^{-2} s^{-1}, but negative responses occur at higher photon fluence rates. At 732 nm only negative responses were measured, even at lower photon fluence rates.

Due to the different shapes of the irradiance-response curves at various wavelengths the relative quantum efficiency could not be used as a measure of the spectral sensitivity of phototaxis for the action spectrum. Therefore, in case of positive phototaxis the reaction values measured at $2.8 \cdot 10^{-10}$ mol cm^{-2} s^{-1} and in case of negative phototaxis the values measured

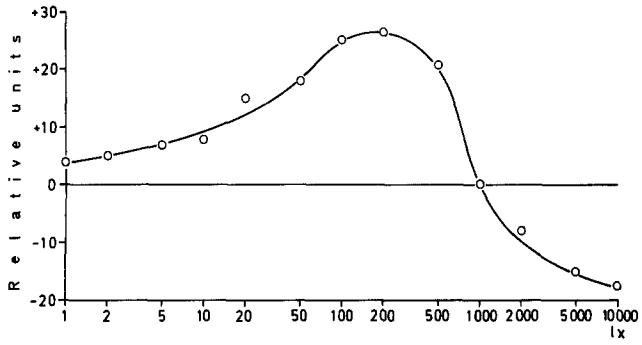

Fig. 3. White light illuminance-response curve of phototaxis. Abscissa: illuminance in lx; ordinate: phototactic effect in relative units

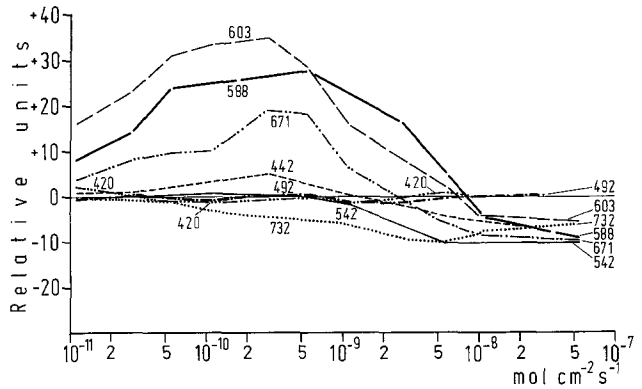

Fig. 4. Phototactic irradiance-response curves measured at following wavelengths: 420, 442, 492, 542, 588, 603, 671 and 732 nm. Abscissa: photon fluence rates in mol cm^{-2} s^{-1}; ordinate: phototactic effect in relative units

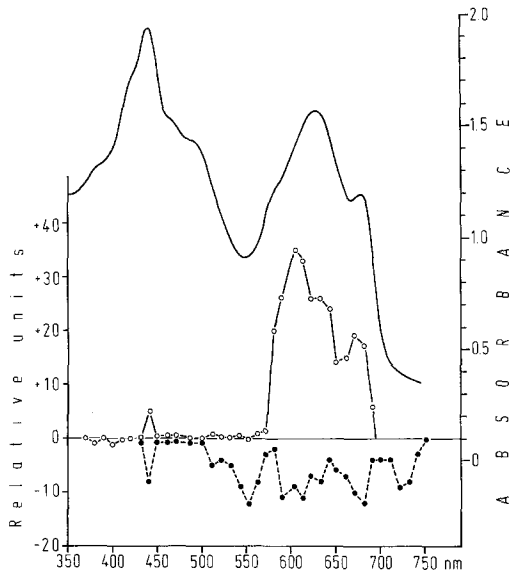

Fig. 5. Action spectra of positive (*open circles, solid line*) and negative phototaxis (*closed circles, dashed line*). For comparison the in vivo absorption spectrum is drawn (*fine solid line*). Abscissa: wavelengths in nm; ordinate: phototactic effect in relative units and absorbance

at $1.12 \cdot 10^{-8}$ mol cm^{-2} s^{-1} were plotted against the wavelengths (Fig. 5). For comparison the in vivo absorption spectrum is drawn in the same figure.

The main maximum of positive phototaxis corresponds with the absorption maximum of C-phycocyanin. Contrary to *Phormidium*, even blue and red light absorbed by chlorophyll *a* is active, represented by smaller but distinct peaks around 440 and 670 nm. A shoulder is found between 620 and 650 nm probably due to allo-phycocyanin absorption. Thus the action spectrum of positive phototaxis indicates that the effective radiation is absorbed by photosynthetic pigments, namely chlorophyll *a* and the phycocyanins.

The same is true with negative phototaxis. However, as mentioned above, radiation of wavelengths between 500 and 560 nm which is inactive at the irradiance levels of positive phototaxis causes clear negative reactions at higher photon fluence rates. Moreover, in red light above 700 nm exclusively negative responses could be observed. Both ranges of wavelengths are little or not absorbed by photosynthetic pigments.

Effect of Inhibitors. The participation of photosynthetic pigments in the absorption of the phototactically active light suggests that the mechanism of phototactic orientation might be coupled with the photosynthetic apparatus somehow. If so, phototaxis should be sensitive to inhibitors of the photosynthetic electron transport, such as DCMU and DBMIB. Tyagi (1976) observed in *Cylindrospermum* an inhibition of phototaxis by CMU at very high concentrations (above 10^{-4} mol), but obviously in these experiments the inhibition of the movement toward the light source was the result of an inhibition of motility rather than of the ability of the trichomes to orient themselves. The effect of 10^{-8} to $5 \cdot 10^{-5}$ mol DCMU on phototactic orientation was studied.

Observations by microscope revealed that the *Anabaena* trichomes orient themselves perfectly well under unilateral illumination even at higher DCMU concentrations. This is true for positive and negative phototaxis as well. These findings are supported by experiments with the population method. Movement toward the light source and, at higher illuminance, away from it is observed even if $5 \cdot 10^{-5}$ mol DCMU is present. Only the inversion point is shifted to a higher illuminance (Fig. 6). Thus, contrary to our expectations the inhibition of the photosynthetic electron transport does not markedly influence the phototactic orientation. The same is true with the plastoquinone anta-

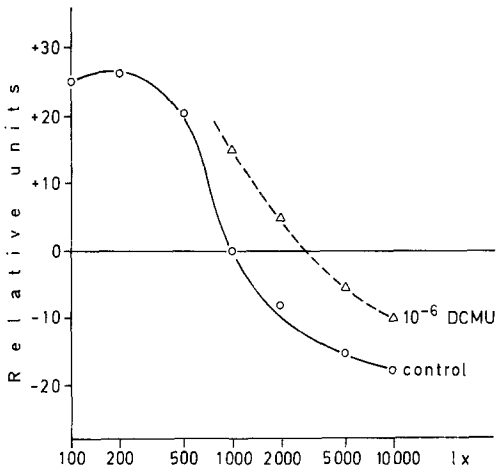

Fig. 6. Effect of DCMU on phototaxis in white light. Abscissa: illuminance in lx; ordinate: phototactic effect in relative units. Control: circles and solid line; 10^{-6} mol DCMU: triangles and dashed line

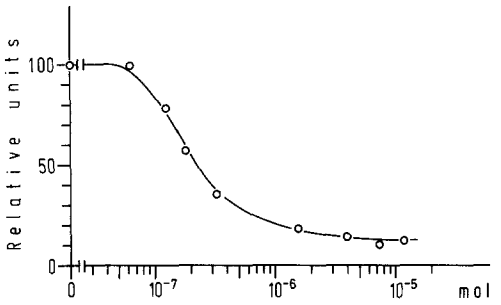

Fig. 7. Effect of DCMU on the photosynthetic O_2-production. Abscissa: DCMU concentration in mol; ordinate: O_2-production in relative units

gonist DBMIB. No effect of 10^{-6} mol DBMIB on phototactic orientation could be observed in white light neither at 200 lx (positive) nor at 5000 lx (negative).

Photosynthesis Measurements. Since in some blue-green algae DCMU obviously does not penetrate the gelatinous sheath (Nultsch, 1974), it needs to be tested whether penetration problems do account for the weak effect of DCMU on phototaxis in this strain. The dose-response curve of the effect of DCMU on the photosynthetic O_2-production (Fig. 7) clearly shows that *Anabaena variabilis* strain B377 is very sensitive to this substance. O_2-production is already affected by concentrations lower than 10^{-7} mol. 50% inhibition is caused by $2.2 \cdot 10^{-6}$ mol. It is noteworthy that even at very high concentrations (up to 10^{-5} mol) a DCMU resistant part of about 12% remains unaffected. Since O_2-production was measured immediately after DCMU application it cannot be excluded that after longer incubation this insensitive part disappears.

These results demonstrate that DCMU certainly penetrates the sheath and the cell wall quite well. This is confirmed by another experiment in which a DCMU solution (0.2 ml, 10^{-4} mol) was rapidly injected into the illuminated algal suspension in the test cuvette of the oxigraph. Photosynthetic O_2-production rapidly decreased and after about half a minute fell below the compensation point.

Discussion

In principle the action spectrum of positive phototaxis of *Anabaena variabilis* resembles that of *Cylindrospermum alatosporum* measured by Tyagi (1976), although the latter one lacks any fine structure due to the broad bands and the little number of filters. The realtively low inversion point of phototaxis in *Anabaena variabilis* enables us to measure even an action spectrum of negative phototaxis. This is of interest because up to now the action spectra of positive and negative phototaxis are known only in a few organisms (Halldal, 1961).

Our experiments have shown that in *Anabaena* the action spectra of both positive and negative phototaxis look alike in so far as radiation absorbed by photosynthetic pigments, chlorophyll *a* and the phycocyanins, is active. A direct coupling between phototaxis and photosynthesis, however, could not be demonstrated. Inhibitors of the photosynthetic electron transport such as DCMU and DBMIB do not affect phototactic orientation even at high concentrations at which they inhibit photosynthetic O_2-production to an extent of about 90%. Therefore, the ineffectiveness cannot be due to impermeability of the cytoplasmic membrane, the cell wall or the sheath for these substances. One could assume that only photosystem I which is rather insensitive to DCMU and DBMIB is involved. However, this is improbable because of the strong effect of light absorbed by the phycocyanins, the bulk of which transfers the energy to photosystem II (Amesz, 1974; Ried et al., 1977).

In negative phototaxis, in addition, radiation between 500 and 560 nm as well as between 700 and 750 nm is effective which is scarcely or not absorbed by the photosynthetic pigments. Searching for other photoeffects induced by radiation of these wavelengths in blue-green algae, we found the following spectra indicating activity of green light: The action spectrum of conversion of phycocyanin into phycoerythrin-precursors of *Tolypothrix tenuis* indicates activity between 480 and 580 nm with a maximum at 541 nm (Fujita and Hattori, 1962). The action spectrum for reversal of photo-induced filamentous growth of

Nostoc muscorum shows activity between 500 and 600 nm with a maximum around 540 nm (Lazaroff and Schiff, 1962; Lazaroff, 1966; see also the review by Lazaroff, 1973). Robinson and Miller (1970) demonstrated for *Nostoc commune* that previously motile trichomes becames sheathed and break into non-motile single cells after irradiation with green light (520 nm) or with minor quantum efficiency in the blue (420–440 nm). This morphogenetic effect was completely reversible by irradiation with red light (maximum 640 nm). The action spectrum for depotentation of phycoerythrin synthesis in the dark of *Tolypothrix tenuis* has a maximum at about 550 nm (Diakoff and Scheibe, 1973). The action spectra for chromatic adaptation in *Fremyella diplosiphon* have maxima at 540 nm for induction of phycoerythrin synthesis and at 650 nm for its reversal (Vogelmann and Scheibe, 1978). In the same organism Haury and Bogorad (1977) found the maxima of phycoerythrin production at 387 and 550 nm. Phycochrome *b* in *Tolypothrix distorta* has one form absorbing maximally near 510 and another form absorbing at 570 nm (Björn and Björn, 1976).

Only two pigment systems absorbing radiation above 700 nm are known: photosystem I and phytochrome. Up to now there is no evidence that one of them is involved in negative phototaxis of *Anabaena*, but a phytochrome like tetrapyrrol may be considered as photoreceptor pigment.

The different action spectra of positive and negative phototaxis indicate the participation of different photoreceptors in both the reactions. Two principal possibilities exist:

1. The photosynthetic pigments are active as photoreceptor pigments of positive and negative phototaxis as well, but in negative phototaxis one or two additional photoreceptor pigments are active which absorb radiation of 500–560 and 700–750 nm. These additional pigments could be a *b*-type phycochrome (500–560 nm) and a phytochrome like pigment (above 700 nm).

2. One or more unknown pigments are active as photoreceptors, which are sensitive to radiation around 440 nm and between 500 and 750 nm. Even in this case phycochromes are possible candiates, since the phycochromes *a*, *b* and *c* described by Björn and Björn (1976) show absorption maxima in the range of wavelengths in question. In this case photosynthetic pigments would function only as shading pigments producing an absorption gradient between the irradiated and the shaded side. The different mechanisms of positive and negative phototaxis, however, cannot be explained this way.

Contrary to Oscillatoriaceae the trichomes of Nostocaceae do not rotate during movement. Therefore, at first view, the bending of the straight trichomes of *Anabaena variabilis* under unilateral illumination seems to be comparable to the phototropic bending of *Tolypothrix* trichomes which is the result of differences in the growth rates of the shaded and the illuminated sides (Manten, 1948). This is improbable because the action spectra of both the reactions are quite different. Whereas in *Anabaena* mainly the range between 500 and 700 nm is phototactically active, the phototropic bending of *Tolypothrix* is caused by irradiation < 500 nm. Moreover, the behaviour of the U formed trichomes can hardly be interpreted this way.

Another explanation could be that the bending of the trichomes is caused by differences in the motive forces at the illuminated and the shaded sides of the filaments. However, these differences cannot be the result of different photokinetic responses of both sides for the following reasons:

1. The white light illuminance-response curve of photokinesis which has been measured in the same way as in the strain B 1403-10 (Nultsch and Hellmann, 1972) shows the optimum at 1000 lx, whereas in the illuminance-response curve of phototaxis the inversion point is already reached at this illuminance (Fig. 3).

2. At lower photon fluence rates, where photokinesis is positive, the trichomes bend toward the light source, although the irradiated side perceives more photons per time and area unit and should therefore move faster than the shaded side. On the other hand, at high photon fluence rates, where the photokinetic effect becomes zero or negative, the filaments bend away from the light source, although now the shaded side should move faster.

3. The action spectrum of photokinesis which has been measured in the same way as in the strain B 1403-10 is quite different from the action spectrum of phototaxis.

From these results we may conclude that phototaxis in *Anabaena variabilis* is brought about by a mechanism of its own, and is the result of neither photokinesis nor a succession of photophobic responses (Diehn et al., 1977).

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