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INTERCELLULAR POWER TRANSMISSION ALONG TRICHOMES OF CYANOBACTERIA

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An attempt at demonstrating lateral power transmission over millimeter distances along a coupling membrane has been undertaken. Trichomes of the multicellular filamentous cyanobacteria *Phormidium uncinatum* were illuminated with a very narrow light beam forming a light spot that covered only 4–5% of a 1–2 mm long cyanobacterial trichome. Such illumination was found to support motility (gliding along agar surface) of the trichome under conditions when the light was the only energy source. It was also shown that illumination with the light spot caused rotation of rings of slime (accompanying the operation of the 'motors' responsible for the motility of cyanobacteria) not only in the illuminated, but also in the distal, nonilluminated part of the trichome. Electric potential transmission along trichomes was revealed by means of the extracellular electrode technique. The light spot was found to induce generation of an electric potential difference between two electrodes in the dark region of the trichomes, which were placed at different distances from the illuminated end. Cutting the trichomes between the light spot and the closest 'dark' electrode abolished this effect. Valinomycin + K^+ and carbonyl cyanide *p*-trifluoromethoxyphenylhydrazone affected the potential difference formation between two 'dark' electrodes much stronger than that between a light and a dark electrode. All the light spot-induced effects develop in the seconds time scale. Both the amplitudes and the kinetics of the potential difference measured with four electrodes placed along the trichome prove to be in good agreement with the theoretical curves computed on the basis of the electric cable equation. It is concluded that transcellular power transmission in the form of $\Delta\psi$ takes place along trichomes of cyanobacteria. This confirms the hypothesis about the biological function of $\Delta\psi$ as a transportable form of energy.

Introduction

Membranes of mitochondria, chloroplasts and bacteria contain enzymes generating a transmembrane difference of H^+ electrochemical potentials ($\Delta\bar{\mu}_H$) composed of electric ($\Delta\psi$) and concentrational (Δ pH) constituents [1]. $\Delta\psi$ proves to be the primary form of $\Delta\bar{\mu}_H$, since the electric capacitance of the membrane is much lower than the pH buffer capacitance of solutions in which the membrane is bathed [2,3]. A $\Delta\psi$, if produced by a $\Delta\ \bar{\mu}_H$ generator localized in a certain area of a membrane, inevitably propagates all over the membrane enclosing a vesicle, i.e., a cell or an organelle. This $\Delta\psi$ propagation can, in principle, be used by living systems as a mode of transmitting power over distances limited by the extent of a membrane-enclosed space. Such a power-transmission mechanism should be much faster than diffusion of ATP or the substrates of respiration and glycolysis (for calcu-

Abbreviations: $\Delta\bar{\mu}_H$, transmembrane electrochemical H^+ potential difference; $\Delta\psi$, transmembrane electric potential difference; DCCD, *N, N'*-dicyclohexylcarbodiimide; FCCP, carbonyl cyanide *p*-trifluoromethoxyphenylhydrazone.

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lation, see Ref. 4). This is the reasoning that underlies an idea that power transmission is one of the biological functions of coupling membranes which in terms of the hypothesis operate, at the level of the cell or organelles, as 'electric cables'. The electric cable hypothesis had been advanced in 1969–1971 [5,6], and was recently reconsidered in connection with the possible functions of giant mitochondria in muscle [7–12] and yeast [13].

Trichomes of multicellular blue-green algae composed of a linear sequence of many hundreds or even thousands of cells could be a suitable subject for studies on lateral power transmission. Each cell of a trichome is surrounded by a cytoplasmic membrane which, like those of other prokaryotes, belongs to the category of coupling membranes bearing $\Delta\bar{\mu}_H$. There is electron microscopic evidence for the existence of very thin intercellular channels (microplasmadesmata) between the trichome-forming cells [14]. Trichomes can be several millimeters long, so $\Delta\psi$ transmission can be studied by the methods of classical electrophysiology. Using extracellular electrodes, Häder [15] observed formation of an electric potential difference between the 'head' and 'tail' parts of *Phormidium uncinatum* trichomes fully exposed to a total illumination. Also, a certain photoelectric response was obtained by means of intracellular electrodes [16].

In this paper, we report results of an investigation of power transmission along trichomes of *P. uncinatum*. Measurements of both the electric responses and motility of trichomes indicate that $\Delta\psi$ produced in a small illuminated part of a trichome is transmitted throughout its length with all the trichchome-composing cells being energized. For preliminary communications, see Refs. 12 and 17.

Materials and Methods

In all the experiments, the filamentous blue-green algae (cyanobacteria) *P. uncinatum* have been used. The cyanobacteria were grown during 24 h at 25°C in a luminostat on the surface of 2% agar containing 0.05 M KNO_3, 0.57 mM K_2HPO_4, 0.14 mM $MgSO_4$, $1.5 \cdot 10^{-5}$ M $FeCl_3$ and $1.5 \cdot 10^{-5}$ M ammonium citrate.

The photoelectric responses of *P. uncinatum* trichomes were measured extracellularly; the method

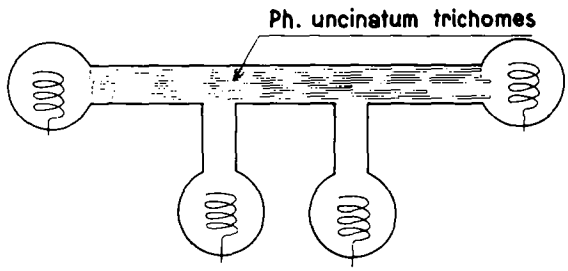

Fig. 1. A chamber for measuring the photoelectric responses of cyanobacteria (for explanation, see text).

was originally used in neurophysiological studies [18] and more recently in experiments with cyanobacteria [15,16]. 10–25 *P. uncinatum* trichomes were put into a groove (length 1.5 mm, depth 0.1 mm) in a plastic plate. At $\frac{1}{3}$ and $\frac{2}{3}$ of its length, the groove was intercepted by two narrower grooves leading to compartments with silver electrodes. The diameter and length of electrodes were 0.5 and 10 mm, respectively. The other two electrodes were placed in compartments linked to ends of the main groove (Fig. 1). The distance between an electrode and trichomes was 2–3 mm. The grooves and the four electrode-containing compartments were filled with distilled water. From the electrodes, the signal was transmitted to an electrometer (input resistance 10^9 Ω) and then to a Disa double-beam oscilloscope. Under these conditions, the time resolution of the measurements was about 1 ms. As a light source, an OI-19 lamp or an argon laser was used.

Results

Light-spot-induced motility of P. uncinatum trichomes

To reveal whether power can be transmitted from cell to cell along a cyanobacterial trichome, the following three approaches were used in this study: (i) measurement of the motility rate of trichomes; (ii) observation of the movement of slime rings excreted by these organisms and (iii) monitoring the photoelectric responses of the cyanobacteria by means of extracellular electrodes. In all the cases, cyanobacterial membranes remained intact during the experiments. This could be important to prevent a possible closing of the intercellular electric contacts arising in response to damage or modification of the mem-

brane. This closing takes place, e.g. in gap junctions connecting certain types of animal cells [19,20].

In this group, it was found [11,21] that the motility (gliding) of cyanobacteria is a $\Delta\bar{\mu}_H$-supported process which is similar to the motility of flagellar bacteria. In particular, the gliding of cyanobacterial trichomes was shown to be supported not only by the naturally generated $\Delta\bar{\mu}_H$ (light or respiration energy were used) but also by the artificially imposed $\Delta\psi$ or ΔpH. So, motility rate can be an intrinsic probe for $\Delta\bar{\mu}_H$ in cyanobacteria. If there is power transmission along the entire trichome due to, e.g., intercellular electric conductance, one may hope that the electric potential difference generated across the cytoplasmic membrane near the end of the trichome can be utilized in its distal part to support operation of the motility mechanisms ('protonic motors').

In the experiments, *P. uncinatum* trichomes were illuminated by a small white light beam forming a spot of light which covered only about 5% of the trichome length. When light was the only energy source for motility, such partial illumination of trichomes was found to induce gliding. The motility rate proved to be similar to that under total illumination, provided the light intensity of the spot was sufficiently high. Addition of $1 \cdot 10^{-4}$ M DCCD, which totally inhibited the light-induced increase in the ATP level in trichomes, did not prevent the light spot-supported motility.

These data seemed to be compatible with the idea of transcellular power transmission in the form of $\Delta\bar{\mu}_H$. However, an alternative explanation of the light spot-induced motility was not ruled out. One could speculate that operation of protonic motors in the part of the trichome under the light spot would prove to be sufficient to support the motility of the entire organism. In such a case, the illuminated part of the trichome would work as a locomotive, while in the rest of the trichome, protonic motors would not be operative.

The evidence against 'the locomotive hypothesis' was furnished by the following experiments. A solid medium (agar) used in the above study was replaced by an aqueous solution. Under such conditions, trichomes were motionless, although the protonic motors were operative. Their action revealed itself in the rotatory motion of rings of slime excreted by cyanobacteria. As the experiments showed, the light spot induced rotation of the slime rings not only in the illuminated, but also in the nonilluminated parts of the trichome, including its distal end. Thus, the light spot activates all protonic motors of this organism. Such an effect should obviously involve intercellular power transmission.

It should be stressed that this power transmission occurred within seconds. This is in agreement with a calculation [4] showing that electric transmission along a 1 mm trichome composed of several hundreds of electrically connected cells must proceed for a time not longer than several seconds, while diffusion of any chemical compound (ATP, glucose or a chemical transmitter) requires many minutes or even hours. The absence of any DCCD inhibition of the above-described light spot-induced effects also indicates that $\Delta\bar{\mu}_H$, rather than ATP or any other chemical product of photosynthesis, is responsible for power transmission.

Direct measurement of the $\Delta\psi$ transmission along cyanobacterial trichomes

In the experiments described in this chapter we tried to apply an orthodox electrophysiological method to monitor a $\Delta\psi$ transmission along *P. uncinatum* trichomes. To this end, a technique for electric current and potential measurement with external (extracellular) electrodes was used.

Cyanobacterial trichomes were put into a groove in a plastic plate. The groove was filled with distilled water and four electrodes were placed close to the trichomes: electrodes 1 and 4 in the vicinity of its opposite ends and electrodes 2 and 3 at $\frac{1}{3}$ and $\frac{2}{3}$ of the trichome length, respectively. When a small part of the trichomes, situated, e.g., close to electrode 3 (Fig. 2) was illuminated with a light beam, a potential difference between the electrodes was found to arise as if there were extrusion of a positively charged species in the illuminated part, the trichome being a unitary electric system with a high electric conductance between cells. $\Delta\psi$ developed within seconds and in some cases reached 10 mV. $\Delta\psi$ proved to be higher, and increased faster, when measured between a light electrode and a dark electrode than between any two dark electrodes (Figs. 2A and 3).

Fig. 3 reveals a good agreement between (i) the amplitudes and kinetics of the experimentally measured $\Delta\psi$ (solid lines) and (ii) those calculated

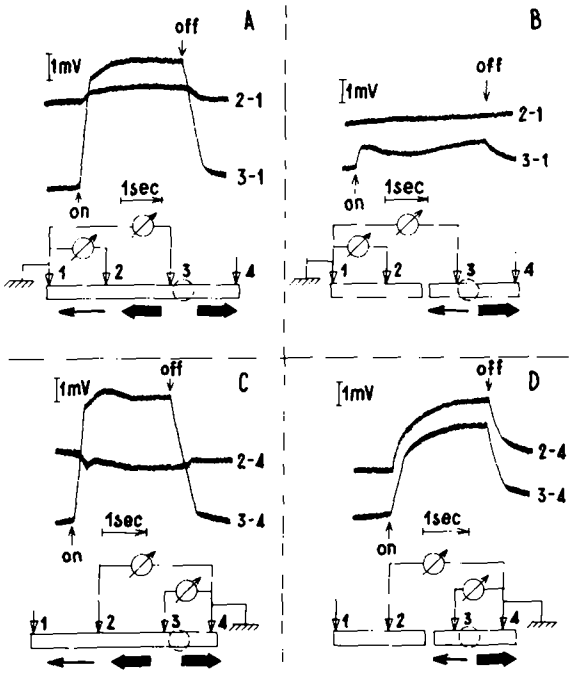

Fig. 2. Extracellular measurement of electric potential transmission along trichomes of *P. uncinatum*. Responses to switching on and off illumination with a narrow light beam are shown. Figures near curves are for electrode numbers. In each of four measurements, A–D, electric potential differences were measured simultaneously between two pairs of electrodes (e.g., in A, between electrode 2 and 1, upper curve, and between electrodes 3 and 1, lower curve). Under experimental curves, schemes of the electric measurements are shown. In the schemes: vertical and horizontal arrows represent electrodes and currents, respectively. Illuminated area is shown by a dashed circle.

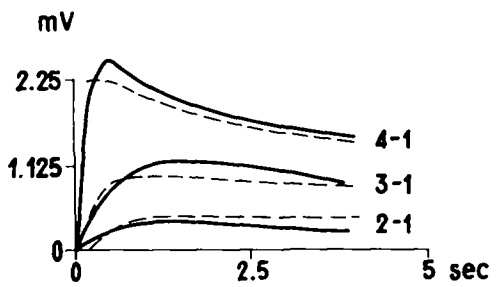

Fig. 3. Comparison of the experimental photoelectric responses of *P. uncinatum* trichomes (———) and theoretical curves computed on the assumption that these trichomes have cable properties (- - - - -). Figures near curves are the number of electrodes. Light spot was localized near electrode 4.

assuming that a cyanobacterial trichome has electric cable properties (dashed lines). The theoretical curves were obtained for a model of a noninductional infinite cable, in a point of which a potential difference is generated. Calculation of the potential difference, V_i, for an isolated cable at a given electrode was done according to Eqn. 1:

$$V_i(t) = V \cdot \left[\phi\left(\frac{x_r}{2} \cdot \sqrt{\frac{RC}{t}}\right) \cdot \phi\left(\frac{x_i}{2} \cdot \sqrt{\frac{RC}{t}}\right)\right] \quad (1)$$

where x_i and x_r are the distances of the generator from the measuring electrode and the reference electrode, respectively; t, the time after switching on the generator; R and C, the longitudinal resistance and capacitance of a 1 cm long trichome, respectively (RC value was calculated from the experiment in Fig. 2); $\phi(y)$, the error function was found from Eqn. 2:

$$\phi(y) = \frac{2}{\sqrt{\pi}} \cdot \int_0^y e^{-y^2} \cdot dy \quad (2)$$

V_i' was obtained for a trichome, of which the specific membrane resistance (R_m) was assumed to be $4 \cdot 10^7$ $\Omega \cdot cm^2$. To this end, Eqn. 3 was used:

$$V_i'(t) = V_i(t) + a \cdot \int_0^t V_i(\tau)\, e^{a\tau} \cdot d\tau \quad (3)$$

where $a = 1/R'C$ and R' is the membrane resistance of a 1 cm long trichome.

Cutting the trichomes between light electrode 3 and dark electrode 2 was found to prevent completely the light-induced generation of $\Delta\psi$ between two the dark electrodes 2 and 1 (Fig. 2B). $\Delta\psi$ appeared again when the light spot was moved to the previously dark end (not shown in the figure). As seen in Fig. 2C, quite a large potential difference between electrodes 3 and 4 develops when the light spot is near electrode 3. Simultaneous $\Delta\psi$ measurement between electrodes 2 and 4 revealed a small potential difference of the opposite direction. This $\Delta\psi$ changed its sign, and its amplitude greatly increased, after the trichome was cut between electrodes 2 and 3 (Fig. 2D). Such an effect could be predicted in terms of the electric cable scheme. Indeed,

H^+ extrusion from trichomes by photosynthetic $\Delta\bar{\mu}_H$ generators in the illuminated trichome part must result in currents (i) between electrodes 3 and 2, and (ii) between electrodes 3 and 4. These two currents are of opposite directions, and the overall current between electrodes 2 and 4 is in fact the difference between currents (i) and (ii). After cutting the trichomes between electrodes 2 and 3, current i disappears. Now only current (ii) contributes to the overall electrode 2–4 current. This must result in the formation of a $\Delta\psi$ of the same direction and magnitude as that between electrodes 3 and 4.

The direction of the photoelectric response can be reversed without cutting trichomes. This took place when the light spot was shifted from one end of the trichome to the other (Fig. 4).

In Fig. 5 the effect of valinomycin is shown. In this experiment, a small amount of KCl ($4 \cdot 10^{-5}$ M) was added to the distilled water in the chamber. This salt concentration proved to be insufficient to increase the medium conductivity to the level preventing the $\Delta\psi$ generation from being measured by

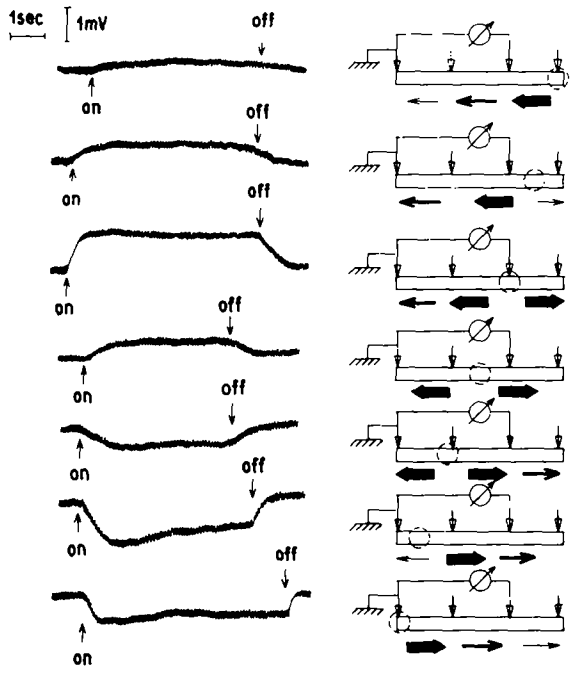

Fig. 4. Photoelectric responses of *P. uncinatum* trichomes scanned with a light beam. For explanation of schemes, see Fig. 2.

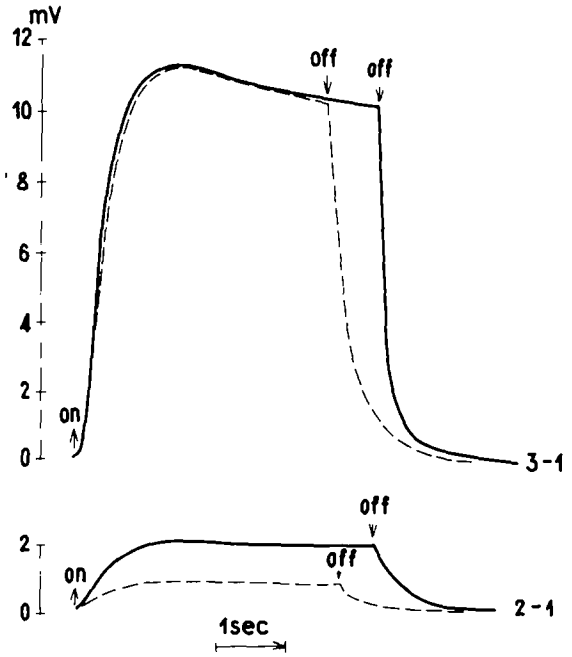

Fig. 5. Effect of valinomycin on *P. uncinatum* photoelectric responses after 3 min treatment of trichomes with valinomycin:(———) before and (– – –) after valinomycin addition. A light spot was situated near electrode 3. The potential differences were measured between electrodes 3 and 1 or 2 and 1. Valinomycin and K^+ concentrations were $1 \cdot 10^{-5}$ and $4 \cdot 10^{-5}$ M, respectively.

the extracellular electrodes. Without valinomycin, illumination by a light spot produced, as usual, an electric potential difference between the light and the

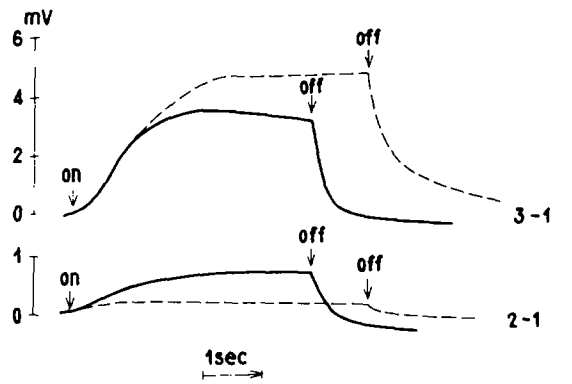

Fig. 6. FCCP effect on *P. uncinatum* photoelectric responses: (———) before and (– – –) after $5 \cdot 10^{-6}$ M FCCP addition. Illumination and measurements as in Fig. 5.

dark electrodes as well as between the two dark electrodes. Addition of valinomycin resulted in a significant decrease in the response measured by the two dark electrodes. The light electrode response changed negligibly. Similar relationships were revealed in the experiments when a protonophorous uncoupler FCCP, instead of valinomycin, was added (Fig. 6).

Addition of DCCD greatly increased the potential difference between the two dark electrodes and also between the light and dark electrodes. The latter effect is shown in Fig. 7A. The same figure is remarkable in one more respect. The duration of the light exposure in this case was 40–50 s, or about 10-fold longer than that in the previous experiments. One can see that after such a long illumination, switching off the light resulted in an overshoot of the photopotential decay. The overshoot could be abolished when the experiment was performed under anaerobic conditions (Fig. 7B).

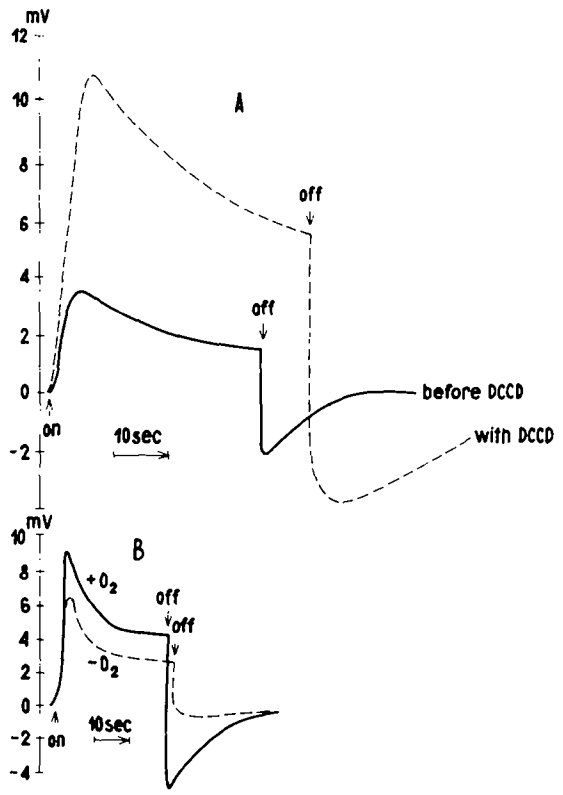

Fig. 7. Effect of DCCD and anaerobiosis on *P. uncinatum* photoelectric responses. DCCD concentration was $5 \cdot 10^{-4}$ M.

Discussion

The results of the two above-described series of experiments, i.e., motility and photoelectric response measurements, can be regarded as independent bodies of evidence of the intercellular transmission of power in the form of $\Delta\psi$. In fact, illumination of a small part of a cyanobacterial trichome gives rise to an electric potential spreading from the illuminated to the dark trichome parts, so that all the protonic motors of the trichome prove to be actuated.

A decisive indication of the intercellular $\Delta\psi$ transmission was obtained when we used two dark electrodes placed at different distances from the light spot. The formation of a light spot-induced electric potential difference between these electrodes cannot be explained without assuming $\Delta\psi$ transmission from the illuminated to the nonilluminated region of the trichome. Cutting the trichome between the light spot and the nearest dark electrode completely abolished the effect of the light spot (see Fig. 2).

Computer analysis of the data gave theoretical curves of the electric potentials of the amplitude and kinetics which closely resembled those found experimentally (Fig. 3).

In this analysis, a trichome was assumed to have electric cable properties. Power transmission along a cable is known to be effective only if the cable is not too long, as an energy loss proportional to the cable length is an inevitable consequence of such transmission. The loss can be calculated in the following way.

The distribution of electric potential, V, along the long axis (x) of a trichome can be determined according to Eqn. 4:

$$V = V_0 \cdot \exp\left(-\frac{x}{\lambda}\right) \tag{4}$$

where V_0 is the transmembrane electric potential difference in the illuminated region of a trichome, and λ the length constant calculated from Eqn. 5:

$$\lambda = \sqrt{\frac{R_m}{R_i} \cdot \frac{d_1 d_2^2}{2(l_1 + d_1)(l_1 d_2^2 + l_2 d_1^2)}} \cdot (l_1 + l_2) \tag{5}$$

where R_m and R_i are the specific resistance of 1 cm^2 of the membrane and of 1 cm^3 of the cytoplasm, and l and d are the length and the radius of the cyanobac-

terial cell (subscript 1) or of intercellular conducting channels (subscript 2), respectively.

By varying these parameters within reasonable limits we can estimate the probable energy loss accompanying power transmission in cyanobacterial trichomes. For example, assuming $R_m = 4 \cdot 10^7\ \Omega \cdot cm^2$, $R_i = 50\ \Omega \cdot cm$, $l_1 = 2\ \mu m$, $l_2 = 0.1\ \mu m$, $d_1 = 3\ \mu m$ and $d_2 = 0.1\ \mu m$, we obtain $\lambda = 1.1$ cm. Under these conditions, the energy loss, i.e., $1 - (V/V_0)$, equal to $1 - \exp(-x/\lambda)$, proves to be less than 5 and about 25% for 0.5 and 5 mm distances, respectively (Fig. 8).

An attractive suggestion is that multicellular cyanobacteria regulate conduction via contacts between cells, as in the case of gap junctions in animal systems. If so, it may be possible to optimize the length of the cable, i.e., to maintain energy dissipation at a reasonably low level. This may be especially important in trichomes of such cyanobacteria as *Oscillatoria princeps* whose length can reach 1 cm. Other filamentous cyanobacteria, and in particular *P. uncinatum*, can form several millimeter long trichomes during prolonged cultivation. To shorten the distance of intercellular power transmission, it is sufficient to have an impermeable junction in the chain of cells connected by means of permeable intercellular contacts.

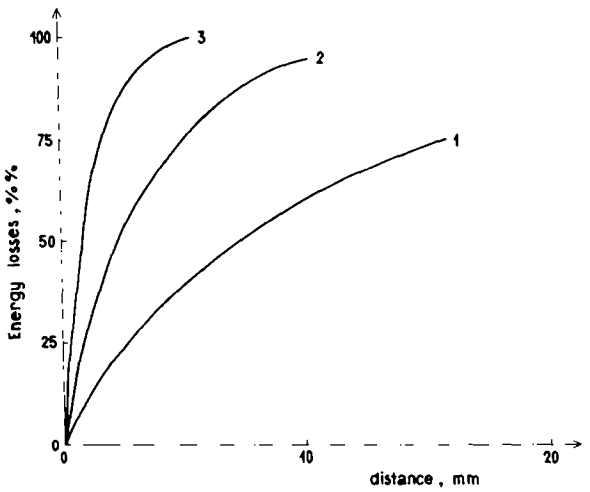

Fig. 8. Energy loss as a function of distance of transmission along cyanobacterial trichomes. Curves 1, 2 and 3, for membrane resistances of $4 \cdot 10^7$, $4 \cdot 10^6$ and $4 \cdot 10^5\ \Omega \cdot cm^2$, respectively.

Such a situation was realized when fluorescein was injected into one of the trichome-composing cells. It was found in this group that fluorescence quickly spread from cell to cell, demonstrating the existence of permeable junctions between individual cells in a trichome. However, sometimes the diffusion of fluorescein suddenly stopped so that a sharp border between the fluorescing and the dark parts of the trichome appeared. Certainly, it is not clear whether the border is impermeable to fluorescein only, or also to small ions and other charged species creating the intercellular electric conductance. If the latter is true, power transmission must be interrupted by a cell separated from the adjacent one by an impermeable border. This confines the $\Delta\psi$ spreading to those distances that are not too long for economical energy transfer.

On the other hand, closing the intercellular junctions may occur in response to damage of the cell into which a microelectrode with fluorescein is inserted. Indeed, isolation of the injured parts of the trichome may be a function of the impermeable borders. If this were the case, power transmission in undamaged trichomes would occur over the entire trichome length.

The effects of valinomycin, FCCP, DCCD and anaerobiosis described in this paper (Figs. 5, 6 and 7A) can be easily explained in terms of the cable concept. Both valinomycin and FCCP can decrease the membrane resistance below its natural level. DCCD, which blocks the H^+ channels of H^+-ATP-synthetase, can increase the resistance. Therefore, valinomycin and FCCP must lower the effectiveness of power transmission along the trichome membrane while DCCD must enhance it. These were just the effects that we observed. As to the influence of anaerobiosis which abolishes an overshoot in the 'off' response after long light exposures, it may be due to the prevention of membrane lipid photooxidation in the illuminated part of trichomes. Using the cable model, one can explain the overshoot by the assumption that a local decrease in the membrane resistance took place under the light spot. Observation of the fluorescence of cyanobacterial pigments showed that 1 min illumination of trichomes with the light intensity equal to that in the light spot resulted in oxygen-dependent changes indicating photooxidation of membranous components.

Recently, the above-described explanation of the overshoot was confirmed by a direct measurement of the electric resistance across the bundle of trichomes. It was found that 1 min light exposure led to a decrease in the resistance. It should be noted that this and other effects of the light described above are not due to a local heating of the system, since they cannot be prevented by a heat filter.

In conclusion, the data reported above can be considered as a precedent of transmission of power in the form of $\Delta\psi$ over millimeter distances along a coupling membrane. Such an energy-transfer mechanism is much faster than diffusion of ATP or other chemical energy carriers as calculated in this group [4].

Transduction of energy into a transmembrane electric potential difference can be a way for living systems to overcome diffusion limitations of certain biochemical processes. Such a mechanism should be especially useful when urgent short-term work must be carried out. For instance, illumination of even a small portion of a trichome which is motionless due to lack of an available energy source to form $\Delta\bar{\mu}_H$ can energize all the protonic motors of the organism. So, the trichome proves to be motile and, due to phototaxis, glides from a dark to an illuminated area.

On the other hand, one should understand that performance of long-term $\Delta\bar{\mu}_H$-linked work requires lateral transport of $H^+(OH^-)$ to prevent formation of local pH gradients. These gradients must inevitably be formed if $\Delta\bar{\mu}_H$ generators and $\Delta\bar{\mu}_H$ consumers are operating in different parts of, e.g., a cyanobacterial trichome, being connected via $\Delta\psi$ transmission only (for a discussion, see Refs. 11 and 12).

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