

Dedicated to Prof. dr. sc. ZVONIMIR DEVIDÉ on the occasion of his 80th birthday

Photomovement in plants and microorganisms: old and new questions

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Photomovement, taken in its broader sense, comprises the responses of motile organisms, intracellular movement, phototropic curvature, and photonastic movement. These responses can be scalar or vectorial with respect to the light direction. For classifying scientific questions, a schematic sequence can be defined, *viz.* perception – signal transduction – terminal response. In this paper, the present state of knowledge is summarized for selected systems exemplifying various types of response. This is intended to provide the background for future scientific questions that appear important and promising to be investigated. Although the modern genetic and molecular approaches are most essential for progress, they have to be based on well-established and sound results from »classical« physiology.

Key words: motile organisms, perception, photonasty, phototaxis, phototropism, sun tracking, signal transduction

Preface

It was in 1967 that one of the earliest meetings of the European photomorphogenesis group was held in Croatia. This meeting at Hvar was excellently organized by Zvonimir Devidé, who also succeeded for the first time to have our group joined by colleagues from Eastern European countries, such as East Germany and even the Soviet Union. In addition, this was a starting point for photobiology to become established in the former Yugoslavia. It should be added that professor Devidé still belongs to a generation with sound knowledge in morphology and cell structure, which are occasionally in danger to be overlooked as the base for all kinds of physiological research, including photobiology. In recognition of his merits, and to thank him once more, this article is dedicated to him on the occasion of his 80th anniversary.

Meinem Freund Zvonimir Devidé in Erinnerung an viele gemeinsame wissenschaftliche und kulturelle Interessen und mit Dank für wertvolle Anregungen gewidmet.

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Introduction

One of the classical fields of photobiology is photomovement, i.e. movement under the control of light. Similarly as in other fields of photobiology, and physiology in general, research on photomovement has recently reached a new dimension, i.e. molecular methods and approaches are being successfully introduced. This may become more evident if we take a look backward at the »state of the arts« that was reached by pure »classical« approaches, and by relating this to contemporary experimental strategies, pointing to unsolved problems that are expected to be solved using the new approaches.

Extensive information on the present state of knowledge, including detailed references to the most recent accomplishments, can be found in the respective chapters of a forthcoming book on photomovement (HÄDER and LEBERT 2001). In the present article, therefore, references are restricted to the past.

Photomovement s.str. designates light-controlled movement of motile organisms (mainly plant and bacterial micro-organisms, but occasionally including protists, which belong to the animal kingdom). Recently, however, the term is also used in its broader sense, to include intracellular movement of organelles and, moreover, light-controlled curvatures of plant organs (photomovement s.l.).

The signal-transduction chain

It is useful to apply a generalized scheme to the various photoresponses (e.g. HÄDER 1979): perception of the signal – signal transduction (signal processing) – terminal response (modulation of movement). This idealized sequence of events has proven to be a useful framework for classifying the scientific questions that are under investigation or that appear worth being investigated.

Perception (input)

Whatever the type of final response, there is a remarkable diversity of photosensory pigments (e.g. NULTSCH 1991 and references therein), ranging from a variety of blue-light absorbing pigments to phytochrome, and occasionally including even chlorophyll which is otherwise only involved in energy harvesting, rather than in information processing. Moreover, for responses that are vectorial with respect to the light source, perception of the light direction is an additional requirement. This is always accomplished by comparison of the light absorption at different sites within a cell or an organ, and several fundamental principles have been discovered in the past decades (cf. KRAML 1994). Nearly all of them imply the pigments' association with cell structures.

Signal transduction (black box)

It was only in the more recent past that photobiologists became aware that there is a black box – a *very black box* – functioning as a necessary link between perception and response. It is postulated that the information of the environmental light signal is transferred to an internal signal – or to a series of internal signals. However, in most cases, the biochemical and/or biophysical nature of those signals is not yet known. One of the most puz-

zling phenomena of signal transduction is energy amplification, a set of mechanisms by which energy-requiring steps can be triggered by signals with extremely low energies. Cascades of internal signals can serve this purpose, and this is a favored domain for genetic and molecular approaches that are beginning to shed some light upon the 'black boxes' (cf. phototropism of *Phycomyces*, p. 126). As an additional complication, vectorial responses of course ought to be linked to vectorial signals by vectorial transduction. This makes signal transduction an extremely complex challenge to modern research.

Response (output)

There is a large diversity of cellular and subcellular structures that underlie the various types of response and the respective motor apparatuses. These range from direct action of cytoskeleton elements to mechanisms for differential growth and turgor regulation in cells or tissues (for the well-established facts see, e.g., the respective chapters in Haupt and Feinleib 1979). At the borderline between transduction and response, specific checkpoints are required, at which the internal signals are channeled into the response system, and at which metabolic energy is fed into the motor apparatus. Here too, the spatially differential control of vectorial movement is a particular challenge for research.

A few old and new questions will be presented for the four fundamental types of photomovement.

Light responses of motile organisms

A century ago, plant physiologists interested in photomovement s.str. were mainly concerned with discriminating between its basic types and defining them by appropriate terms. Much progress has since been made, and the response types have been clarified, thus opening the door to research on causal relationships. Usually, three types of responses are defined, viz. photokinesis, the photophobic response and phototaxis (cf., e.g. HÄDER 1979).

Photokinesis

The *steady-state* velocity depends on the fluence rate (intensity) of the light and can, in the ideal case, be expressed by a well-defined function without hysteresis, i.e., there is no adaptation. In some organisms, photokinesis is directly dependent on the current photosynthetic energy (NULTSCH 1991). In the more interesting cases, however, this response is triggered by a true low-energy light signal, thus requiring amplification processes.

Photophobic response

Upon a change in fluence rate (light-on or step-up, light-off or step down), a *transient* change in velocity is observed, frequently starting with a stop response followed by reversal of movement. Afterwards, the velocity returns to its former level, even in a different fluence rate, and there is no relation to the direction of the light signal. It should be emphasized that velocity is a vectorial term, comprising speed and direction. Between taxonomic groups there are large differences concerning the contribution of speed and direction to the overall response (NULTSCH 1991).

Recently, an additional type of photophobic response has been discovered in *Halo-bacterium halobium*. In this species, the more/less rhythmical autonomous reversals of the direction of movement are speeded up or delayed by light-on (step-up) or light-off (step-down) signals depending, among other things, on the wavelength of the light. Accordingly, several types of bacteriorhodopsin have been established as photoreceptor pigments by modern genetic approaches (cf. SCHIMZ et al. 1983), but the signal transduction chain is still open for research, as are details of the action of the motor apparatus, in this case rotation of the flagellum, as typical for bacteria in general. – It is almost certain, however, that this particular system cannot serve as a model for photophobic responses in eucaryotes.

In any case, the transience of response requires an effective adaptation, with a time constant larger than that of the change in signal intensity, and this is a particular challenge for research. Progress in bacterial chemotaxis may serve as a basis for the respective research on the photophobic response. It will then be a particular challenge to investigate whether taxonomically different systems make use of common, or at least similar, steps in the signal transduction chain which may, in some cases, include changes in transmembrane potentials and ion fluxes (e.g. HAUPT and HADER 1994).

Phototaxis

The overall direction of movement is controlled by the light direction. This results in accumulation towards, or away from, the light source. The great diversity of photosensory pigments mentioned above is particularly found in phototaxis. Most spectacular was the discovery that rhodopsin serves this function in the phytoflagellate *Chlamydomonas*, a result corroborated by modern genetic approaches (FOSTER et al. 1984, cf. also HEGEMANN 1991). As to the signal transduction chain, recent biophysical approaches appear promising (e.g., MARANGONI et al. 1996).

Widely open questions concern the perception of the light direction. The absorption gradient, necessary for directional perception, can be based either on spatial comparison of the light intensities at two or more receptor sites, or on temporal comparison at only one site, at which the absorbance changes as the movement proceeds (FEINLEIB 1980). Although much knowledge has accumulated in the past, it remains to be clarified in detail how the (spatial or temporal) absorption gradient is generated. Obviously, there are fundamental differences between taxonomic groups. Most puzzling is the perception of the incident angle of light by a flat cell such as the desmid *Micrasterias*, which orients perpendicular or parallel with respect to the light beam, depending on additional factors (NEUSCHELER 1967).

Phototactic accumulation can be brought about by precise steering as in some phytoflagellates. However, little is known yet about the spatial control within the motor apparatus, e.g. of the differential interaction of dynein and tubulin in the flagellum.

One of the less precise and less direct ways of orientation is the trial-and-error mechanism of gliding cyanobacteria (e.g., *Phormidium*, NULTSCH 1975) which modulate their more/less rhythmic autonomous reversals in such a way that one gliding direction with respect to the light source is preferred, and thus random accumulation toward, or away from, the light source ensues. This requires the filaments to discriminate whether the light is coming from their advancing or their trailing end. This implies a steadily changing front-rear

polarity. Whether this discrimination resides in individual cells or is somehow integrated over the whole filament is a question that still needs »classical« physiological research before molecular approaches appear promising.

Light-controlled movement of cell organelles

There are two types of light-controlled movement of cell organelles:

Photodinesis

The rotational movement of the cytoplasm (cyclosis) is controlled by light (induction, acceleration, retardation). In most cases, the chloroplasts participate in this movement, but their average overall distribution in the cell remains unchanged (SEITZ 1979). As the light direction has no effect, photodinesis is a strictly scalar response. In addition to photoperception in the cytoplasm, pigments in the chloroplasts may also contribute to the perception, and the interaction of these inputs is an open question.

Orientalional movement of chloroplasts

Chloroplasts orient relative to the light direction by rearrangement or repositioning. Usually, this is interpreted as a temporal adaptation to the light environment, to ensure optimal light harvesting and to minimize photodamage.

In early times, chloroplast orientation was thought to represent »phototaxis« of chloroplasts in their cytoplasmic »environment« (e.g. HAUPT 1959). However, it is now generally accepted that the light signal and its direction is not perceived by the organelles, but by the surrounding cytoplasm, which controls the organelles' movement (cf. WADA et al. 1993). In consequence, the term »phototaxis of chloroplasts« is now disappearing.

More than a century ago, it was already known that various taxonomic groups can differ in their spectral sensitivity, and this can also be true for different responses in the same species. With classical physiology, this diversity of photosensory pigments has been confirmed. Moreover, in some systems, a single response can be triggered independently by two or more photosensory pigments, or the interaction of two sensory pigments may be necessary (e.g., the »low-intensity response« and the »high-intensity response« in the alga *Mougeotia scalaris* with phytochrome and »cryptochrome« as the respective sensory pigments, WADA et al. 1993). This raises the question as to the convergence of the separate signal transduction chains and to the master reaction that collects the different flows of information and controls the final response (cf.: respective discussion in HAUPT 1999).

As to the signal transduction chains, a number of likely steps have been proposed, as deduced from experiments in a number of model systems, including biophysical approaches. However, all these steps (e. g., calcium/calmodulin, changes in membrane properties, reorganization and anchoring of cytoskeleton elements) are still under »pro and con« discussion, as the respective observations cannot yet prove that these processes are integral parts of the flow of information rather than side effects, and their causal interrelationships need to be disentangled (cf. WADA et al 1993, HAUPT and HÄDER 1994):

The motor apparatus is almost certainly the actin-myosin system, at least in most of the examples investigated so far. In detail, however, there are indications for some diversity

concerning the particular way of action. The open questions also comprise the possible points of attack for the controlling »internal signals« within the signal transduction chain(s). These questions are a particular challenge because of the directionality and multiplicity of the signal transduction chains. Moreover, a contribution of other cytoskeleton elements, in addition to actin and myosin, to the movement can so far not be excluded (cf. WADA et al. 1993). However, from recently started molecular approaches, progress can be expected at all three levels, i.e.: for open problems in perception, signal transduction and the function of the motor apparatus, and first results have already been reported (cf. WINANDS and WAGNER 1996).

Phototropism

Phototropism is curvature of cells or organs in response to the light direction. In most of the model systems under investigation, this orientation is toward the light (positive phototropism). The response is usually the result of unequal growth of opposite flanks, i.e., of opposite cell-wall regions in unicellular organs or of opposite tissues in multicellular organs.

The sporangiophore of *Phycomyces* is a good example for the use of increasingly sophisticated methods. In his pioneering physiological studies, BUDER (1918) discovered that the sporangiophore acts as a collecting lens, thus establishing an absorption gradient opposite to the light direction. This initiated photobiological research in *Phycomyces*. The next important step ensued when Delbrück applied cybernetic models to the sporangiophore in order to relate phototropism to the differential light-growth response (DELBRUCK and REICHARDT 1956). This was one of the earliest successful examples for biocybernetics as a new discipline. Afterwards, progress in the genetics of *Phycomyces* opened the door for mutant analysis in phototropism (e. g.. OOTAKI et al. 1973, CERDÁ-OLMEDO and MARTIN-ROJAS 1996). Formally, several steps of the signal transduction chain could be defined by the discovery that various independent photoresponses, including phototropism, are controlled by a single photoreceptor and that, vice versa, the bending response can also be induced by external signals other than light, both results requiring that the signal transduction chains have some steps in common. Now, these steps need to be characterized in terms of biochemical and/or biophysical reactions.

More complex is phototropism in multicellular organs. After the basic work of DARWIN (1880), etiolated grass coleoptiles became the favored system, particularly oat (*Avena*), later on followed by corn (*Zea*). In the fifties, it appeared that the main problems in phototropism had been solved, with a flavin compound as the photoreceptor pigment and with carotenoids as shading pigments for generating the absorption gradient, which is necessary for sensing the light direction. Furthermore, unequal auxin distribution was thought to be the second messenger, resulting in unequal growth, in accord with the repeatedly (and sometimes tacitly) modified CHOLODNY-WENT theory.

Today, the nature of the photoreceptor substance as a flavin can be considered proven, generalizing from *Arabidopsis* (see below; CHRISTIE et al. 1999). Otherwise, however, this very simple model recently became questioned at nearly all levels (FIRN 1994; there also a summary of the historical aspects). The distribution of sensitivity along the coleoptile as well as the basis for the absorption gradient across the organ turned out to be more complex

after the discovery of strong longitudinal light piping through the coleoptile (MANDOLI and BRIGGS 1984). Moreover, the role of auxin as the most important internal signal is questioned again, calling for reinvestigation of signal transfer. And finally, the analysis of unequal growth at opposite flanks as the terminal response requires more detailed knowledge at the cellular level than simple measurements of the integral responses of the whole organ can provide (FIRN 1994). The role of the cytoskeleton in growth responses belongs to the modern perspectives (e.g. NICK 1999).

Genetic and molecular approaches at all levels of the signal transduction chain have been initiated in *Arabidopsis thaliana*, and this thoroughly studied plant is becoming a central model system for phototropism (BRIGGS and LISCUM 1997, CASHMORE 1997). A spectacular first result is the discovery of phototropin, a dual-chromophoric flavoprotein that serves as the photosensory pigment for phototropism, a mechanism which likely applies to other plant species as well (CHRISTIE et al. 1999).

A particular phenomenon of phototropism is »sun tracking«, by which the leaves of higher plants orient towards the sun and keep this orientation during his way over the firmament, by continuous bending in the horizontal and the vertical directions, also including torsions. This sun tracking is a complex phenomenon, as curvature can be based mainly on growth or on turgor changes, and perception and/or response can reside either in the lamina or in the pulvini (KOLLER et al. 1990). Thus, sun tracking is becoming a new field of research with its own problems, e. g.: By what mechanism can a leaf discriminate between obliquely incident light beams impinging toward the top or toward the base of the leaf? How are asymmetrical signals transduced asymmetrically? Finally and most puzzling: what mechanism is behind those cases in which, during the night and in the absence of any obvious external stimuli, the leaf orients towards the direction of sun rise, thus »anticipating« this direction (KOLLER 2000). What is the respective »memory«?

Photonastic movement

Photonasty designates movement of cells or organs which is controlled by light, but does not show any relation to the light direction. Concerning the mechanism, the contribution of turgor changes is prevailing as compared to growth; hence, photonastic movements are usually reversible. Two main phenomena are being investigated in more detail: the folding/unfolding of leaves and the opening/closing of stomata.

The folding/unfolding of leaves can be under the direct control of light signals, but it can also be controlled by the physiological clock: and in some plants external signals other than light are important, e.g. mechanical stimulation. On the one hand, this makes those systems more complicated; on the other hand, there are additional points for experimental attack on the basic mechanisms.

The main past and present research concerns the mechanism of turgor changes. Whereas, in earlier times, the anatomy and histology of the respective tissues has been worked out, recently the causality at the cellular and subcellular levels is under investigation. Particularly the contribution of ion channels and ion pumps and their control appear to be the key for understanding differential turgor changes in the motor tissues (cf. KOLLER 2000 and references quoted therein).

The opening/closing of stomata is based on turgor changes in the guard cells and, to some degree, also in the subsidiary cells. In a similar fashion as discussed above for the folding/unfolding responses of leaves, stomata movement is also complicated by the fact that several factors can contribute to it. This already applies to the light signal, as there are at least two separate photoreceptor systems, viz. »cryptochrome« and photosynthetic pigments, which may trigger completely different and interacting, or competing, signal transduction chains. In addition to light, water potential, intracellular CO₂ concentration, and phytohormones impact on stomatal aperture. All these signals can compete, or mutually support, each other, and light effects operate in part *via* a feedback system including changes of water potential and/or CO₂ levels (e. g. RASCHKE 1979, ZEIGER 1990). It is thus a major, but difficult, task to analyze this most complicated multifactorial network.

Concluding remarks

This short survey was to show that decades of so-called classical research have established amazingly firm foundations, but that further progress now depends more and more on »modern« genetic and molecular approaches. This can be considered a feed-back system, as the latter approaches are promising only if backed up by the respective »classical« results that are available to very different degrees, in different fields of photomovement. In other words, results obtained by classical methods are necessary to be able to ask meaningful questions to be approached by molecular techniques; and the results obtained frequently call for additional »classical« experiments.

Such a combination of »old« and »new« approaches may also be promising for elucidating a phenomenon that has only recently been found to be more than an exception. As repeatedly mentioned in this article, there are cases in which a given response is under the control of multiple signal transduction chains. How far can this be generalized, and what are the mechanisms for the respective integrations?

On the other hand, there are problems in photomovement for which the question »classical or modern« is not yet relevant: the ecological significance of the responses. In this respect, most data are available for stomata movement. It appears evident that interaction of the controlling factors has to ensure an optimal compromise between most effective light harvesting for photosynthesis on the one hand, and surviving in adverse conditions on the other hand (cf. ZEIGER 1994). In other types of photomovement, the ecological significance is not always so obvious as it appears at first sight. These questions are important if the evolution of those responses is to be understood.

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