Book Reviews

Phototransformations

Phytochrome. Proceedings of a symposium, Eretria, Greece, Sept. 1971. K. Mitrakos and W. Shropshire, Jr., Eds. Academic Press, New York, 1972. xiv, 632 pp., illus. $21.50.

Lectures on Photomorphogenesis. H. Mohr. Springer-Verlag, New York, 1972. xii, 238 pp., illus. Paper, $14.80.

The plant pigment phytochrome exists in two forms, P_r (red absorbing) and P_{fr} (far-red absorbing), interconvertible by light. Only P_r is present when a seedling is underground, but some phytochrome molecules are converted to P_{fr} as soon as the seedling reaches the light. P_r and P_{fr} function as the two poles of a switch used by the plant to turn metabolic reactions on and off in response to light signals from the environment. P_{fr} is the active form.

Phytochrome response has been reported in the algae, mosses, liverworts, ferns, gymnosperms, and angiosperms, that is, in all major groups of plants except the fungi. The list of morphological responses known to be under phytochrome control is equally impressive and encompasses all the major stages in plant development from embryogenesis to senescence.

In 1971, 20 years after the discovery of phytochrome, a phytochrome institute organized by K. Mitrakos and sponsored by NATO and the University of Athens, was convened in Eretria, Greece. The primary purpose was to review phytochrome research of the past two decades, and many workers actively engaged in such research summarized work in their fields. Twenty-three lectures were presented and are now published in the book *Phytochrome*. Studies of phytochrome's biological significance and of its chemistry, phototransformations, thermal reactions, and purification are included. This is an excellent review of virtually all the important phytochrome research prior to 1971.

The first chapter, by H. A. Borthwick, describes the early experiments leading to the discovery of phytochrome, performed by Borthwick, S. B. Hendricks, and co-workers at the U.S. Department of Agriculture station in Beltsville, Maryland. A series of action spectra of seemingly disparate phenomena revealed unexpected similarities. A brief flash of red light (action peak at 660 nm) during an otherwise dark period promoted floral initiation in *Xanthium* plants, germination in lettuce seed, and leaf expansion in dark-grown pea seedlings. Furthermore, potentiation by red light could be reversed by subsequent far-red light (action peak at 730 nm), and this sequence could be repeated for several cycles without diminution of effect. With remarkable insight, these scientists predicted that a single pigment exists in two forms: red light converts it to P_{fr} and far-red light to P_r. Absorbance measurements made with a double-beam spectrophotometer confirmed their predictions. The pigment was isolated in 1959 and the predicted absorbance changes were detected in vitro. Even those who know the story well should find this chapter worth reading, for Borthwick successfully recreates the atmosphere of excitement that existed as each experiment brought the investigators closer to discovering the photoreversible pigment phytochrome.

How are light-induced changes in chromophore structure transduced to biological responses? Several approaches are discussed. The pigment has been isolated from a variety of plants, and Rüdiger compares the purification procedures of different investigators. Molecular weights ranging from 26,000 to 375,000 have been reported, leading some workers to postulate the existence of several phytochrome species. Briggs, Gardner, and Hopkins present a different explanation for this apparent anomaly: some plants such as oats contain large amounts of a protease that cleaves phytochrome into smaller photoreversible units. These authors describe purification techniques that minimize proteolytic degradation.

Lhoste presents a theoretical analysis of molecular mechanisms that might be involved in phytochrome phototransformations. Rüdiger has attempted to separate the phytochrome chromophore from the protein moiety, and he proposes a model for the chromophore and its linkage to the protein. Butler discusses photochemical properties of the pigment in vitro. Haupt provides experimental evidence that phytochrome is localized on or near the plasmalemma and has a dichroic orientation that changes direction during photoconversion. His technique involves irradiation of the alga *Mougeotia* with a microbeam of polarized red or far-red light which alters the orientation of its single large chloroplast. Black and Vlitos discuss possible relationships of phytochrome and plant hormones, and Schopfer and Smith analyze phytochrome control of enzyme synthesis and activity. Mitrakos discusses phytochrome mediation of carbohydrate metabolism.

In addition to regulating growth and development, photochrome photoconversions also control rapid reversible responses such as ion movements, leading one to question whether the phytochrome system acts on one reaction common to all these responses. Borthwick proposes that phytochrome does just one thing wherever it acts: it alters membrane permeability. Schopfer argues that phytochrome acts in many different ways, and one way is as an "on" and "off" switch for the transcription of selected genes. The latter viewpoint is vigorously espoused by Hans Mohr in his book *Lectures on Photomorphogenesis.* Mohr and co-workers at the University of Freiburg studied the effects of light on enzyme synthesis and on 22 different biochemical, histological, and morphological changes in dark-grown mustard seedlings. These studies provide most of the experimental evidence on which Mohr's book is based.

Some of the growth responses described by Mohr are potentiated by brief red irradiation and prevented by subsequent far-red irradiation, the usual criteria for phytochrome mediation. However, irradiation with high-intensity far-red light for several hours is far more effective than a brief red treatment in some reactions, such as synthesis of phenylalanine ammonia-lyase and ascorbate oxidase. These responses are intensity-dependent even after a photostationary P_{fr} level has been established. The question of whether these high-intensity reactions (HIR) are also mediated by phytochrome, alone or in conjunction with another pigment, has evoked considerable interest. Some investigators believe that photosynthesis is involved in HIR, but Mohr unequivocally rejects this view. He proposes that phytochrome is the sole photoreceptor for HIR, and he reasons as follows: Although red light converts 80 percent of phytochrome to P_{fr}, the level drops after the irradiation since P_{fr} is destroyed by a dark reaction. Destruction of phytochrome following P_r-to-P_{fr} conversion has been reported by several investigators. Far-red light converts only 2.5 percent of phytochrome to P_{fr}, but this level can be maintained during several hours of irradiation. Mohr contends that 2.5 percent of P_{fr} for several hours is more effective than a higher P_{fr} level for a shorter period. He explains the intensity dependence by proposing that high-intensity light produces an excited species of P_{fr} which is required for some reactions, although other reactions such as lipoxygenase synthesis are promoted by P_{fr} in the ground state. This hypothesis, developed by Mohr's former colleague Hartmann, is one of many detailed explanations presented by Mohr to account for the complex effects of light on morphogenesis.

Unfortunately, Mohr fails to give a balanced view of photomorphogenic concepts, since he lacks objectivity when presenting the views of those who hold opposing theories. He pays scant attention to the membrane theory of phytochrome action, despite considerable evidence in support of it. However, his in-depth study of photomorphogenesis in a single organism, the mustard seedling, is instructive, his analysis creative, and his presentation clear and forthright. His book, together with the proceedings volume, summarizes the vast amount of phytochrome lore acquired during two decades of intensive research. These books also reveal the large gaps in knowledge of the molecular events that transduce light energy to biological response. They should stimulate scientists from a wide variety of disciplines to use their skills to solve this fascinating problem.

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Basic Evolutionary Processes

Animal Cytology and Evolution. M. J. D. WHITE. Third edition. Cambridge University Press, New York, 1973. viii, 962 pp., illus. $55.

Although it is customary to distinguish between the Darwinian and neo-Darwinian facets of evolutionary interpretation, few scientists would deny that evolution is the grand strategy of life, operating in time and space and through the medium of mutations, chromosomal changes, and differential reproduction. It is recognized further that evolution, when viewed in all its varied aspects, is an extraordinarily complex affair, operating at many levels and open to investigation by a wide variety of techniques and procedures.

White is well aware of these complexities, and he has continued, in this third edition of his well-known book, to focus his attention on what he maintains is the essential basis of evolution, namely the cytogenetic process and all that is implied by that term. To phrase it differently, evolution in his view depends, initially and fundamentally, on the changing structure and functional realization of the heritable blueprints of organisms—genes, chromosomes, and transmission mechanisms—and the manner by which these blueprints come into being and are preserved or altered through time. As the title of the volume implies, White confines himself in great measure to the evolutionary processes as they occur or have occurred in the animal kingdom. His evidence is drawn very largely from the insect world, and within the insect world the Orthoptera provide a substantial amount of the factual and illustrative material upon which his views are based. Cytogenetic information from the plant world is mentioned only peripherally or incidentally. This might suggest that a strong bias permeates the volume, but such is not evident to this reviewer. The author, in fact, makes it abundantly clear that the cytogenetic basis of evolution is not only complex but also extraordinarily flexible and exploitable, having, in his words, "an evolution of its own [which] somehow underlies the outwardly visible evolution of phenotypes." Among the many types of cytogenetic processes and events White describes are those which are rare or, often, unique. To some their rarity may indicate their relative unimportance in the general sweep of evolution, but for the particular group of organisms in which these events have become fixed they have provided evolutionary success, however temporary or lasting that success may be. The author, therefore, is fully justified in stating that "cytogenetics . . . cannot endorse any view of evolution in which there is no place for unique, or at any rate very rare, events."

This edition, like the two previous ones, is indispensable to anyone who has an in-depth interest in the basic nature of the evolutionary processes. It is essentially a reference book, addressed to the serious investigator and not to the casual student. The quantity of data presented and examined in detail is enormous. Not everyone will agree with all of White's specific interpretations or perhaps even with his overall contentions, but the more than 3000 references will enable the reader to check original sources when questions arise. It is good to have the volume available; it would also be good if someone could do similarly with the mass of information available from the plant kingdom. It is to be regretted that the cost of this volume will undoubtedly restrict the widespread use it deserves.

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Foraminifera

Distribution and Ecology of Living Benthic Foraminiferids. JOHN W. MURRAY. Crane, Russak, New York, 1973. xiv, 274 pp., illus., + plates. $24.75.

Foraminifera, perhaps the most widespread and surely the most popular microfossils, traditionally have been the subject for ecologic studies by geologists, with a view toward "the present as a key to the past." A book on the distribution and ecology of living Foraminifera therefore potentially has great interest for all paleoecologists concerned with how the fossil record is produced.

The handsomely printed volume at hand has 22 chapters, six of which are directly relevant to such general paleoecologic interests. One of these chapters consists of a useful review of the biology and autecology of living forams; the other five (about four pages each) give short sketches of such topics as