PHOTORECEPTORS AND PLANT DEVELOPMENT

Proceedings of the Annual European Photomorphogenesis Symposium
held at Antwerpen, Belgium

July 22-28, 1979

edited by
J. De Greef
1980
Chapter 1: INTRODUCTION

REMEMBRANCES OF PHYTOCHROME TWENTY YEARS AGO. 3
Butler, W.L.
University of California, San Diego, U.S.A.

THE HISTORY OF PHYTO–PHOTO–SCIENCE.
(NOT TO BE LEFT IN SKOTO TOTO AND SILENCE) 9
Björn, L.O.
University of Lund, Sweden.

Chapter 2: CHARACTERIZATION OF PHOTORECEPTOR PIGMENTS

A BLUE LIGHT PHOTORECEPTOR SYSTEM IN HIGHER PLANTS AND FUNGI. 17
Briggs, W.R.
Carnegie Institution of Washington, Stanford, California, U.S.A.

SPECTROPHOTOMETRICAL PROPERTIES OF PEA PHYTOCHROME IN CYTOSOLIC AND PARTICULATE FRACTIONS. 29
Furuya, M. and Y. Shimazaki
University of Tokyo, Japan.

SPECTROPHOTOMETRIC EVIDENCE FOR A PHOTOCHROMIC REGULATOR IN THE FUNGUS SPHAEROBOLUS STELLATUS. 41
Björn, L.O.
University of Lund, Sweden.
STRUCTURE AND REACTIVITY OF THE PHYTOCHROME CHROMOPHORE. 47
Brandlmeier, T., I. Blos and W. Rüdiger
University of Munich, Germany.

WHAT MAKES THE MOLECULE OF P_R FORM PHYSIOLOGICALLY ACTIVE? 55
Song, P.S. and T.A. Cha
Texas Tech. University, U.S.A.

PHOTOCONVERSION OF PHYTOCHROME BY SHORT RED FLASHES IN MOUGEOTIA AND AVENA. 59
Kraml, M.
University of Erlangen, Germany.

BLUE LIGHT–INDUCED ABSORBANCE CHANGES IN MEMBRANE PREPARATIONS FROM CORN COLEOPTILES. 67
Caubergs, R. and W.R. Briggs*
University of Antwerpen, Belgium, * Carnegie Institution of Washington, Stanford, California, U.S.A.

PREPARATION, CHARACTERIZATION, AND UTILIZATION OF ANTISERUM AGAINST ZUCCHINI PHYTOCHROME. 69
Cordonnier, M.-M. and L.H. Pratt
University of Georgia, Athens, U.S.A.

PHYTOCHROME AND PHYCOBILIPROTEINS WITH CHEMICALLY MODIFIED CHROMOPHORES. 79
Kufer, W., T. Brandlmeier and H. Scheer
University of Munich, Germany.

NANOSECOND FLASH PHOTOLYSIS OF PHYTOCHROME (P_R). 83
Braslavsky, S.E., J.I. Matthews, H.J. Herbert, J. de Kok, C.J.P. Spruit* and K. Schaffner
Max-Planck Institute, Mühlheim, Germany, * Agricultural University, Wageningen, The Netherlands.
CONFORMATIONAL HETEROGENEITY AND PHOTOCHEMICAL CHANGES OF BILIVERDIN DIMETHYL ESTERS IN SOLUTION. 89
Braslavsky, S.E., A.R. Holzwarth, E. Langer*, H. Lehner*, J.I. Matthews and K. Schaffner
Max-Planck Institute, Mülheim, Germany, * University of Vienna, Austria.

Chapter 3: METHODOLOGY OF DETECTION

PHYTOCHROME PURIFICATION AND ASSAY. 103
Pratt, L.H.
University of Georgia, Athens, U.S.A.

IMMUNOFLUORESCENCE LOCALIZATION STUDIES OF THE PR AND PFR FORMS OF PHYTOCHROME IN THE COLEOPTILE TIPS OF OATS, CORN AND WHEAT. 121
Epel, B.L.*, W.L. Butler**, L.H. Pratt*** and K.T. Tokuyasu**
* Tel-Aviv University, Israel, ** University of California, San Diego, U.S.A., *** University of Georgia, Athens, U.S.A.

BOUNDARY CONDITIONS FOR MATHEMATICAL MODELS IN PHOTO-MORPHOGENESIS. 135
Fukshansky, L. and H. Mohr
University of Freiburg, Germany.

THE PHYTOCHROME SYSTEM IN LIGHT- AND DARK-GROWN DICOTYLEDONEOUS SEEDLINGS. 145
Jabben, M., B. Heim and E. Schäfer
University of Freiburg, Germany.

A COMPARISON OF SOME METHODS FOR ESTIMATING PHYTOCHROME CHANGES IN LIGHT-GROWN TISSUES. 159
Vince-Prue, D., A.M. Jose and B. Thomas
Glasshouse Crops Research Institute, Littlehampton, U.K.
IV

IRRADIATION—ENHANCED PHYTOCHROME PELLETABILITY : FILTRATION AND MIXING EXPERIMENTS WITH AVENA. 167
Quail, P.H. and W.R. Briggs
Carnegie Institution of Washington, Stanford, California, U.S.A.

LOCALIZATION OF PHYTOCHROME IN ETIOLATED BEAN HOOKS. 169
Verbelen, J.P., J. De Greef, E. Moereels and E. Spruyt
University of Antwerpen, Belgium.

Chapter 4 : PLASTID DEVELOPMENT

THE PROTOCHLOROPHYLL(IDE) SYSTEM IN CHLOROPLAST DEVELOPMENT. 175
Alhadeff, M., R. Coronado, N. Figueroa and J.A. Schiff
Brandeis University, Waltham, Massachusetts, U.S.A.

SHORT-TERM FAR RED REVERSIBILITY OF RED POTENTIATED CHLOROPHYLL ACCUMULATION IN BEAN. 179
Spruit, C.J.P.
Agricultural University, Wageningen, The Netherlands.

LIGHT-MEDIATED CONTROL OF CHLOROPHYLL FORMATION IN SEEDLINGS OF PINUS SYLVESTRIS. 185
Kasemir, H., S. Schröder and A. Steinhilber
University of Freiburg, Germany.

CONTROL BY PHYTOCHROME OF CHLOROPHYLL SYNTHESIS IN SEEDLINGS OF SORGHUM VULGARE. 199
Sawhney, S., H. Oelze-Karow and H. Mohr
University of Freiburg, Germany.
PHYTOCHROME—INDUCED APPEARANCE OF m—RNA ACTIVITY FOR
THE APOPROTEIN OF THE LIGHT—HARVESTING CHLOROPHYLL a/b
PROTEIN OF BARLEY (HORDEUM VULGARE). 203
Apel, K.
University of Freiburg, Germany.

PROTOCHLOROPHYLL(IDE) AS THE PHOTORECEPTOR FOR THE
LIGHT MEDIATED ONSET OF 5-AMINOLEVULINATE APPEARANCE
IN MUSTARD COTYLEDONS. 205
Ford, M. and H. Kasemir
University of Freiburg, Germany.

IS THERE A REGULATORY EFFECT OF RED LIGHT DURING GREEN-
ING OF SCENEDESMUS MUTANT C-2A’? 209
Brinkmann, G. and H. Senger
University of Marburg, Germany.

INFLUENCE OF PHYTOCHROME UPON MITOCHONDRIAL ACTIVITIES
DURING GREENING. 219
Hampp, R. and A.R. Wellburn*
Technical University of Munich, Germany, * University of Lancaster, U.K.

DETERMINATION OF CHLOROPHYLLS, SAPONINS AND PROTEINS
IN SEPARATED PROLAMELLAR BODIES AND PROTHYLAKOIDS OF
ETIOLATED AVENA SATIVA. 229
Lütz, C. and U. Männing
University of Cologne, Germany.

PIGMENT ACCUMULATION AND PLASTID ULTRASTRUCTURAL
CHANGES IN DARK GROWN CUCUMBER SEEDLINGS. 237
Moran, R., T. Arzee and D. Porath
Tel-Aviv University, Israel.

DEVELOPMENT AND PROPERTIES OF ETIOPLASTS AS INFLUENCED
BY THE PHYTOCHROME SYSTEM. 241
Kraak, L.H. and C.J.P. Spruit
Agricultural University, Wageningen, The Netherlands.
ON THE CHLOROPLAST DEVELOPMENT IN *BETA VULGARIS* VAR. SACCARINAE. 249

Gyldenholm, A.O., P.S. Kibsgaard, B. Stougaard, C. Sundquist* and H. Virgin*
University of Aarhus, Denmark, * University of Göteborg, Sweden.

STUDIES ABOUT THE EFFECT OF PHYTOCHROME ON THE DEVELOPMENT OF THE CAPACITY FOR PHOTOPHOSPHORYLATION AND FOR CHLOROPHYLL SYNTHESIS IN MUSTARD SEEDLING COTYLEDONS. 253

Oelze-Karow, H. and H. Mohr
University of Freiburg, Germany.

PHOTOREGULATION OF Δ-ALA DEHYDRATASE IN RADISH COTYLEDONS. 257

Balangé, A.P. and C. Lambert
University of Rouen, France.

INDUCTION OF Δ-AMINOLEVULINATE SYNTHESIZING ACTIVITY BY LIGHT. 261

Girnth, C., S.P. Gough and C.G. Kannangara
Carlsberg Laboratory, Copenhagen Valby, Denmark.

PHYTOCHROME AND CHLOROPLAST DEVELOPMENT IN PRIMARY LEAVES OF *PHASEOLUS VULGARIS*. 269

Akoyunoglou, G.A.
Nuclear Research Center "Demokritos", Athens, Greece.

LIGHT EFFECTS IN NORFLURAZON TREATED BEAN PLANTS. 285

De Greef, J. and M. De Proft
University of Antwerpen, Belgium.
RAPID PHYTOCHROME ACTIVATION OF NITRATE REDUCTASE IN MUSTARD COTYLEDONS — IS IT AN ARTEFACT? 293
Starr, R., S. Gupta and J. Acton
The Flinders University of South Australia, Australia.

SELECTIVE PHYTOCHROME EFFECT ON TWO MICROSOMAL CYTOCHROME P-450-LINKED MONOOXYGENASES. 297
Benveniste, I., J.P. Salaün, R. Reichhart and F. Durst
Louis Pasteur University, Strasbourg, France.

NON-PHOTOMORPHOGENETIC DEVELOPMENT OF DARK- AND LIGHT-GERMINATED RICE SEEDLINGS ON NITRATE UNDER ANAEROBIOSES. 305
Kordan, H.A.
University of Birmingham, U.K.

PHYTOCHROME MEDIATED TRANSCRIPTION AND TRANSLATION DURING FERN SPORE GERMINATION. 309
Zilberstein, A., J. Gressel*, T. Arzee and M. Edelman
Tel-Aviv University, * Weizmann Institute of Science, Israel.

PHOTOREGULATION OF A PEROXIDASE ACTIVITY AND PRIMARY EVENTS OF THE FLORAL INDUCTION IN SPINACH LEAVES. 311
Karege, F., C. Penel and H. Greppin
University of Geneva, Switzerland.

PHYTOCHROME-MEDIATED INDUCTION OF ASCORBATE OXIDASE AS AFFECTED BY LIGHT PRETREATMENTS. 317
Lercari, B.*, H. Drumm and H. Mohr
University of Freiburg, Germany, * University of Pisa, Italy.

INTERACTION BETWEEN PHYTOCHROME AND BLUE LIGHT PHOTO-RECEPTOR IN BETALAIN SYNTHESIS IN THE SEEDLINGS OF AMARANTHUS CAUDATUS VAR. VIRIDIS. 329
Kochhar, V.K., S. Kochhar and H. Mohr
University of Freiburg, Germany.
Hartmann, E., K. Schmid and M. Nestler
University of Mainz, Germany.

PROBLEMS IN ESTABLISHING A PHYTOCHROME MODULATION OF CYCLIC AMP–LIKE COMPOUNDS. 351
Brennecke, A. and J. Acton
The Flinders University of South Australia, Australia.

Chapter 6: PHOTOCONTROL OF SEED GERMINATION

PHYTOCHROME CONTROL OF SEED GERMINATION IN RELATION TO NATURAL SHADING. 357
Frankland, B. and W.K. Poo
University of London, Queen Mary College, U.K.

PHOTOCONTROL OF KALANCHOË BLOSSFELDIANA SEED GERMINATION. 367
Fredericq, H., R. Rethy, A. Dedonder, J. De Greef* and E. De Petter
University of Gent, * University of Antwerpen, Belgium.

SHORT–TERM REACTIONS OF PHYTOCHROME : FLASH INDUCTION OF SEED GERMINATION IN LACTUCA SATIVA. 375
Scheuerlein, R.
University of Erlangen, Germany.

Chapter 7: LIGHT EFFECTS AND GROWTH REGULATORS
STUDY OF THE BLUE AND RED LIGHT ACTION IN AMARANTHUS SECTIONS. 383
Obrenović, S.
University of Belgrade, Yugoslavia.

RELATIONSHIP OF LIGHT AND GROWTH REGULATORS IN THE PHOTOTROPIC REACTION IN DWARF PEA STEMS. 393
Naunović, G., M. Nešković and D. Grubišić
University of Belgrade, Yugoslavia.

PHOTOREGULATION OF THE DEVELOPMENT OF FUNARIA HYGROMETRICA PROTONEMAS COMBINED WITH A CYTOKININ TREATMENT. 399
Naef, J. and P. Simon
University of Geneva, Switzerland.

PHOTOCONTROL OF MAIZE COLEOPTILE SENSITIVITY TO EXOGENOUSLY APPLIED G A3. 405
Warner, T.J., J.D. Ross and J. Coombs
University of Reading, U.K.

INTERACTION BETWEEN PHYTOCHROME AND EXOGENOUS GIBBERELLIN. 413
Konjević, R.*, E. Schäfer and H. Mohr
University of Freiburg, Germany, * University of Belgrade, Yugoslavia.

STUDY ON THE INTERACTION OF LIGHT AND LIMITING PHYSIOLOGICAL FACTORS ON THE ETHYLENE PRODUCTION BY GREEN MARCHANTIA POLYMORPHA THALLI. 423
University of Gent, * University of Antwerpen, Belgium.

PRELIMINARY SCREENING EXPERIMENTS ON THE EFFECTS OF LIGHT AND GA3 ON THE GERMINATION OF DIFFERENT SEED SPECIES. 431
Dedonder, A., R. Rethy, E. De Petter, H. Fredericq and J. De Greef*
University of Gent, * University of Antwerpen, Belgium.
MORPHOGENIC EFFECTS IN DECAPITATED, ETIOLATED BEAN SEEDLINGS.

De Greef, J., R. Van Hoof and H. Van Onckelen
University of Antwerpen, Belgium.

Chapter 8: MODE OF ACTION

PHYTOCHROME: THE FIRST FIVE MINUTES FROM P_{FR} FORMATION.

Quail, P.H.
University of Wisconsin-Madison, U.S.A.

PHYSIOLOGICAL AND BIOCHEMICAL STUDIES OF PHYTOCHROME ACTIVATION.

Epel, B.
Tel-Aviv University, Israel.

ARE THERE TWO SITES OF PHYTOCHROME ACTION?

Mohr, H., H. Drumm, R. Schmidt and B. Steinitz
University of Freiburg, Germany.

EARLY EFFECTS OF PHYTOCHROME IN LEMNA.

Kandeler, R., H. Löppert, Th. Rottenburg and E. Scharfetter
Agricultural University, Vienna, Austria.

MULTIPLE ACTION OF PHOTOSENSORS AND PATTERN FORMATION IN MUTANT LINES OF Arabidopsis.

Kranz, A.R.
University of Frankfurt/Main, Germany.

Chapter 9: THE PHOTOCONTROL OF VEGETATIVE GROWTH AND FLOWERING
INHIBITION OF HYPOCOTYL GROWTH IN LIGHT AND DARK GROWN *SINAPIS ALBA* L. SEEDLINGS: THE EFFECT OF AN INDUCTIVE PULSE.  
Beggs, C.J., W. Geile, M.G. Holmes, M. Jabben, A.M. Jose and E. Schäfer  
University of Freiburg, Germany.  

CONTINUOUS LIGHT ACTION SPECTRA IN LIGHT AND DARK GROWN *SINAPIS ALBA* L.  
Beggs, C.J., M.G. Holmes, M. Jabben and E. Schäfer  
University of Freiburg, Germany.  

CONTROL OF HYPOCOTYL GROWTH IN GREEN *CHENOPODIUM RU-BRUM* L. SEEDLINGS.  
Holmes, M.G. and E. Wagner  
University of Freiburg, Germany.  

RAPID PHOTOMODULATION OF STEM EXTENSION IN LIGHT–GROWN *SINAPIS ALBA*.  
Morgan, D.C., T.M. O'Brien and H. Smith  
University of Leicester, U.K.  

DEMONSTRATION WITH FIBER ILLUMINATION THAT *PHARBITIS* PLUMULES ALSO PERCEIVE FLOWERING PHOTINDUCTION.  
Gressel, J., A. Zilberstein*, D. Porath* and T. Arzee*  
Weizmann Institute of Science, *Tel-Aviv University, Israel.  

THE CONTROL OF HYPOCOTYL EXTENSION BY BLUE LIGHT.  
Thomas, B.  
University of Reading, U.K.  

PHYTOCHROME MEDIATED ENDOMITOSIS IN *SINAPIS ALBA*.  
Van Oostveldt, P.  
University of Gent, Belgium.  

LEAF UNROLLING IN TWO BARLEY MUTANTS.  
Atkinson, Y.E., J.W. Bradbeer and B. Frankland*  
University of London, King's College, *Queen Mary College, U.K.
ECOLOGICAL RESPONSES OF PLANTS TO DAY—TIME VERSUS END—OF—DAY CHANGES IN THE R/FR RATIO. 551
Kadman-Zahavi, A.
The Volcani Center, Bet Dagan, Israel.

EFFECT OF LIGHT ON THE CALLUS CELLS OF THE MOSS PHYSCOMITRIUM. 557
Menon, M.K.C., I. Grasmück and E. Hartmann
University of Mainz, Germany.

PHYTOCHROME AND INTERNODE ELONGATION IN CHENOPODIUM POLYSPERMUM L. THE LIGHT FLUENCE RATE DURING THE DAY AND THE END—OF—DAY EFFECT. 571
Lecharny, A. and R. Jacques
Laboratoire du Phytotron, Gif-sur-Yvette, France.

Chapter 10 : LIGHT EFFECTS AND RHYTHMS

RHYTHMS AND TIMING — A REVIEW 579
Klein, A.O.
Brandeis University, Waltham, Massachusetts, U.S.A.

THE SEISMONASTIC LEAF MOVEMENT OF MIMOSA PUDICA AND THE NYCTINASTIC LEAF MOVEMENT. 599
Vanden Driessche, T.
University of Brussels, U.L.B., Belgium.

RHYTHMIC PHOTORESONSES IN SEEDLINGS OF SINAPIS ALBA L. 617
Jose, A.M. and E. Schäfer
University of Freiburg, Germany.

AUTHOR INDEX
PHYTOCHROME AND PHYCOBILIPROTEINS WITH CHEMICALLY MODIFIED CHROMOPHORES

Kufer, W., T. Brandmeier and H. Scheer.
Institut für Botanik, Universität, Menzinger Str. 67, 8000 München 19,
W. Germany

Phytochrome (P), the photomorphogenic reaction center pigment, contains a linear tetrapyrrolic chromophore covalently bound to the protein (Grombein et al., 1975; Klein et al., 1977). The photochemistry and the subsequent dark reactions of P are governed, however, by non-covalent protein-chromophore interactions. We have studied these interactions by chemical modification of the chromophore, using phycocyanine (PC) and allophycocyanine (APC), phycobiliproteins with chromophores structurally nearly identical to Pr, as models. Since there exists no satisfactory method for a reversible cleavage of the chromophores in biliproteins, a selective chromophore modification has been carried out with the chromophores still bound to the protein. In fully denatured biliproteins, e.g. in the presence of 8 M urea, the non-covalent interactions are abolished, and the chromophores then react with suitable reagents similar to free bilins. Sodium dithionite, a reducing agent applied for in the dark reversion of Pr to P (Mumford & Jenner, 1971), is such a reagent, known to reduce bilindiones at the central methine bridge to produce bilirubin type pigments (structure C) (Fischer & Plieninger, 1942). The modified pigments can then be renatured, to yield modified native pigments (Kufer & Scheer, 1979a,b). For comparison, the native pigments have been subjected to the same reagent, too.

The reactions carried out with PC are summarized in Fig. 1. One essential result was, that denatured PC could be fully reduced by dithionite, but native PC only partially. When denatured reduced PC was renatured, reoxidation occurred even in the presence of dithionite, and the products obtained this way resembled spectroscopically those produced by treatment of native PC with dithionite in the proper concentration. Thus, the protein changes the thermodynamic properties of the chromophores, e.g. the stability to dithionite differs in the native and denatured state. This effect is possibly related to the conformational change of the chromophore from a type B to a type A geometry during the folding of the protein to its native state (Scheer & Kufer, 1977).

Likewise, Fig. 2 can be drawn for phytochrome, but renaturation was not possible in this case. A similar change in stability for the Pr chromophore is suggested, however, by analogy from the similar spectroscopic data, and the dithionite
Fig. 1: Reaction scheme for the denaturation — renaturation and dithionite — reduction — reoxidation studies carried out with C-phycocyanin (PC) from *Spirulina platensis*.

The schematic formulas represent the probable geometries of the tetrapyrrole skeleton in its three different states.

A extended conformation, typical for native PC and P<sub>r</sub> (Scheer & Kufer, 1977).

B cyclic-helical conformation, typical for denatured PC and P<sub>r</sub> (Scheer & Kufer, 1977) and for free bilindiones (Falk et al., 1978; Lehner et al., 1978; Sheldrick, 1976).

C ridge-tile conformation, typical for 10,22-dihydrobilindiones ("bilirubins") (Bonnett et al., 1978).

Phycocyanorubin (P<sub>PCß20</sub>) obtained by saturating reduction of native PC or renaturation of denatured, reduced PC contains both type A and type C chromophores. Similar schemes have been obtained, too, for allophycocyanin isolated from the same organism and phycoerythrin from *Phormidium persicinum*. 
concentration dependence of the formation of the reduced product. Treatment of native Pfr with dithionite results in dark reversion to Pr, as observed earlier (Mumford & Jenner, 1971). In addition, the positive peak at 418 nm, in the difference spectrum (Fig. 3) indicates, that Pr thus obtained is in equilibrium with a species containing reduced chromophores, and is possibly produced via this species. Since the dark reversion of Pfr has been suggested to be catalyzed by reducing agents, kinetic studies should give more information on the mechanism of this reaction.

The positive bands correspond to formation of Pr (λmax = 660 nm, "reversion") accompanied by the formation of bilirubin-type chromophores (λmax = 420 nm).

**ACKNOWLEDGEMENTS**

This work was supported by the Deutsche Forschungsgemeinschaft. We thank Ms. C. Bubenzer and Mr. C. Harzer for skilful technical assistance.

**REFERENCES**


