Photomorphogenesis in Plants and Bacteria
3rd Edition
Function and Signal Transduction Mechanisms

Edited by

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This book is dedicated to

**Hans Mohr,**

a founding member of the AESOP (Annual European Symposium of Photomorphogenesis),

on the occasion of his 75th anniversary (May 11th 2005).
Plants as sessile organisms have evolved fascinating capacities to adapt to changes in their natural environment. Arguably, light is by far the most important and variable environmental factor. The quality, quantity, direction and duration of light is monitored by a series of photoreceptors covering spectral information from UVB to near infrared. The response of the plants to light is called photomorphogenesis and it is regulated by the concerted action of photoreceptors.

The combined techniques of action spectroscopy and biochemistry allowed one of the important photoreceptors – phytochrome – to be identified in the middle of the last century. An enormous number of physiological studies published in the last century describe the properties of phytochrome and its function and also the physiology of blue and UV-B photoreceptors, unidentified at the time.

This knowledge was summarized in the advanced textbook “Photomorphogenesis in Plants” (Kendrick and Kronenberg, eds., 1986, 1994).

With the advent of molecular biology, genetics and new molecular, cellular techniques, our knowledge in the field of photomorphogenesis has dramatically increased over the last 15 years.

In 2002 the publisher approached us with a suggestion to start a new edition of this advanced textbook. After several discussions we came to the conclusion that a new edition containing only the novel observations would no longer be useful as a textbook. Clearly, all the new molecular information has not erased the validity of the “old” physiological and biochemical data. Even more importantly, it is most unfortunate that in the new generation of researchers the knowledge of the “old” data starts to get lost. Consequently, ample evidence can be found in the literature for over or underinterpretation of results obtained by applying state of art methodologies which can be traced back to lack of in-depth knowledge of classical physiological data.

Therefore, in agreement with the publisher we decided to edit a new textbook focusing on the novel observations and at the same time suggesting the 2nd edition of Photomorphogenesis in Plants (Kendrick and Kronenberg, eds.) to be still available for the interested and motivated reader.

In this new textbook the basis of the physiology and molecular biology of photomorphogenesis is once again summarized in a few introductory chapters, to support the reading of the new chapters. Nevertheless, reading the 2nd edition is strongly recommended.

The world’s leading experts from Europe, Japan, South America and the USA were invited to contribute to this advanced textbook and we are very pleased that almost all of them immediately accepted our invitation.

Despite enormous advances the primary molecular function of photoreceptors is still not known and the UV-B photoreceptor still remains to be identified. Nevertheless, this book attempts to guide the reader through the approaches made with the aim of elucidating how absorption of light by the photoreceptors will be converted into a biochemical signal which then triggers molecular events at cellular level leading to characteristic physiological responses underlying photomorphogenesis of the plant.
Molecular biology, transgenic work, genetics, biochemistry and cell biology techniques have dramatically increased our knowledge in the field of photomorphogenesis. We hope that students, postdocs and academic teachers, like in the past, will again favourably respond to the fascination of photomorphogenesis research and that reading the book in the post-genomic era will stimulate new creative research in this field.

Last but not least we would like to thank the publisher, especially Jacco Flipsen, for his strong support and interest, Prof. Govindjee for invitation and encouragement for this project and Dr. Erzsebet Fejes and Birgit Eiter for excellent assistance in editing.

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<td>amplified fragment-length polymorphism</td>
</tr>
<tr>
<td>APRR</td>
<td>Arabidopsis pseudo response regulator</td>
</tr>
<tr>
<td>ATP</td>
<td>adenosine triphosphate</td>
</tr>
<tr>
<td>B</td>
<td>blue light</td>
</tr>
<tr>
<td>BBP</td>
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<td>early flowering 3</td>
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<td>EPR1</td>
<td>early phytochrome responsive 1</td>
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<tr>
<td>FAD</td>
<td>flavin adenine dinucleotide</td>
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<tr>
<td>FDD</td>
<td>fluorescence differential display</td>
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<tr>
<td>FKF1</td>
<td>flavin-binding kelch repeat F-box 1</td>
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<td>FLC</td>
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<td>Fphs</td>
<td>fungal Phys</td>
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<td>FR</td>
<td>far-red</td>
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<tr>
<td>FSBA</td>
<td>fluorosulfonylbenzoyladenosine</td>
</tr>
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<td>FT</td>
<td>flowering locus T</td>
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<tr>
<td>G</td>
<td>green light</td>
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<tr>
<td>GA</td>
<td>gibberelin acid</td>
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<tr>
<td>GAF</td>
<td>cGMP phosphodiesterase/adenyl cyclase/FhlA</td>
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<td>GAI</td>
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<tr>
<td>GFP</td>
<td>green fluorescent protein</td>
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<tr>
<td>GGDEF</td>
<td>Gly/Gly/Asp/Gly/Phe motif</td>
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<td>GI</td>
<td>gigantea</td>
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<td>GRAS</td>
<td>GAI/RGA and SCARECROW</td>
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<td>HAMP</td>
<td>HK/adeny1 cyclases/methyl-binding proteins/phosphatases domain</td>
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<td>Hd</td>
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<td>HIR</td>
<td>high irradiance response</td>
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<tr>
<td>HKD</td>
<td>histidine kinase domain</td>
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</table>
HKRD histidine kinase-related domain
HO heme oxygenase
HPT histidine phosphotransferase
HWE His/Try/Asp
HY5 hypocotyl 5
ICGs interchromatin granul clusters
LFR low Fluence Response
LHCB light harvesting chlorophyll a/b-binding protein
LHY late elongated hypocotyl
LlAC light-induced absorbance change
LKP2 LOV kelch protein 2
LRE light-responsive regulatory element
LUC luciferase
Me-Ac methyl-accepting chemotaxis protein domain
Mg-ProtoMe Mg-Protoporphyrin IX monomethyl ester
MS mass Spectroscopic analysis
MTHF methylenetetrahydrofolate
NAI2 nitrate reductase
NDPK2 nucleoside diphosphate kinase 2
NLS nuclear localisation signal
NMR nuclear magnetic resonance
NO nitric oxide
NOE nuclear overhauser effect
NPA 1-naphthylphthalamic acid
NPH non-phototropic hypocotyl
Nuc nucleus
ORF open reading frame
PAC PAS-like domain C-terminal to PAS
PAS Per/Arndt/Sim
PCB 3(Z)-phycocyanobilin
Pchlide protochlorophyllide
PEB phycoerythrobilin
PER period
PFT1 phytochrome flowering time 1
Phy phytochrome
PIF3 phytochrome interacting factor 3
PIL1 PIF3-like 1
PIL2 PIF3-like 2
PIL4 PIF3-like 4
PIL6 PIF3-like 6
PIN1 pinformed 1
PKS1 phytochrome kinase substrate 1
PKS2 phytochrome kinase substrate 2
PLD PAS-like domain
PM plasma membrane
PP pyrimidine-pyrimidinone dimers
PP2C protein phosphatase-2C
Proto protoporphyrin IX
PYP photoactive yellow protein
PhiB 3(Z)-phytochromobilin
QTL quantitative trait loci
R red light
RAP2 red light aphototropic 2
RGA repressor of ga 1-3
RGL RGA-like
RNAi RNA interference
<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Full Form</th>
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<tr>
<td>ROS</td>
<td>reactive oxygen species</td>
</tr>
<tr>
<td>RR</td>
<td>response regulator</td>
</tr>
<tr>
<td>Rubisco</td>
<td>ribulose-1,5-bisphosphate carboxylase/oxygenase</td>
</tr>
<tr>
<td>SAP</td>
<td>sequestered areas of phytochrome</td>
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<tr>
<td>SCF complex</td>
<td>Skp1 cullin F-box protein</td>
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<tr>
<td>SCN</td>
<td>suprachiasmatic nucleus</td>
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<tr>
<td>SOC1</td>
<td>suppressor of overexpression of co 1</td>
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<tr>
<td>SPA1</td>
<td>suppressor of phyA 1</td>
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<td>SPY</td>
<td>spindly</td>
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<td>SRD</td>
<td>serine-rich domain</td>
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<td>SRR1</td>
<td>sensitivity to red light reduced</td>
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<td>TC-HK</td>
<td>two-component histidine kinase</td>
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<td>TIC</td>
<td>time for coffee</td>
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<td>TIM</td>
<td>timeless</td>
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<td>TIR3</td>
<td>toll interleukin resistance domain cotaining protein</td>
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<td>toc1</td>
<td>timing of cab expression 1</td>
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<td>ULI</td>
<td>UV-B light insensitive</td>
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<tr>
<td>ULI3</td>
<td>UV-B light insensitive 3</td>
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<tr>
<td>UV</td>
<td>ultra violet light</td>
</tr>
<tr>
<td>UV-A</td>
<td>320-400 nm UV</td>
</tr>
<tr>
<td>UV-B</td>
<td>280-320 nm UV</td>
</tr>
<tr>
<td>UV-C</td>
<td>&lt;280 nm UV</td>
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<tr>
<td>VLFR</td>
<td>very low fluence response</td>
</tr>
<tr>
<td>ZT</td>
<td>zeitgeber time</td>
</tr>
<tr>
<td>ZTL</td>
<td>zeitlupe</td>
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</table>
Color plate section

Chapter 7, Figure 5. Histochemical localization of the expression patterns of PHYB::GUS (a-c) and PHYD::GUS (d-f) promoter-reporter fusion genes in Arabidopsis. (a, d) seven day old dark-grown seedlings; (b, e) seven day old light-grown seedlings; (c, f) flowers.
**Chapter 9, Figure 1.** Localisation of PHYA-GFP fusion proteins in Arabidopsis seedlings. 4d old dark-grown Arabidopsis seedlings expressing fusion proteins of Arabidopsis PhyA and GFP controlled by the Arabidopsis promoter were irradiated briefly with white light. Subsequently bright-field images (greyscale) and confocal images of GFP (green channel) and chlorophyll (red channel) fluorescence have been recorded with a Zeiss LSM510 microscope. The colour-combined images are showing the hook area and an area of the rim of a cotyledon (inlet). Bar= 25 µm.

**Chapter 9, Figure 2.** Model of the light-driven intracellular dynamics of phytochrome A. In dark-grown seedlings phyA is synthesized in its physiological inactive Pr-form (Pr) and stays in the cytosolic compartment. Irradiation establishes a wavelength-dependent equilibrium of the Pr to the active Pfr form. Red light (R) leads to formation of about 80% of Pfr, far-red light (FR) to about 3% Pfr. PhyA Pfr localises to sequestered areas of phytochrome (SAP) in the cytosol and is imported into the nucleus where it forms nuclear speckles. The light-requirements for these intracellular processes overlap with the light requirements for typical physiological responses of phytochrome A. While pulses of light can promote very low fluence response (VLFR, here the effect of a red pulse is shown), continuous irradiation with far-red light (cFR) leads to high irradiance responses (HIR). Due to the instability of the Pfr form of PHYA, continuous red-light (cR) leads to a rapid destruction of the photoreceptor.
Chapter 9, Figure 3. Co-localisation of Phytochrome B with the bHLH factor PIF3. 4d old dark-grown Arabidopsis seedlings simultaneously expressing fusion proteins of PhyB with YFP and PIF3 with CFP each controlled by the 35S promoter were irradiated briefly with white light. Subsequently, confocal images of YFP (green channel) and CFP (red channel) fluorescence have been recorded with a Zeiss LSM510 microscope. The images are showing epidermal cells of the base of a cotyledon, either representing the PhyB-YFP or PIF3-CFP signals, an overlay of these images resulting in yellow colour for co-localisation of PhyB and PIF3 or an additional co-localisation analysis of both factors using ImageJ software package (NIH).

Chapter 9, Figure 4. Localisation of a fusion protein consisting of Arabidopsis PhyB, GFP and a nuclear localisation sequence. 4d old dark-grown Arabidopsis seedlings expressing fusion proteins of Arabidopsis PhyB, GFP and the SV 40 NLS under the control of the Arabidopsis promoter were analysed either after incubation for 24 hours in red light (R) or darkness (cD). Subsequently, bright-field images (greyscale) and confocal images of GFP (green channel) and chlorophyll (red channel) fluorescence have been recorded with a Zeiss LSM510 microscope. The colour-combined images are showing the hook area or an area of a cotyledon. Bar = 25 µm.
Chapter 12, Figure 1. Domain structures for phototropins 1 and 2.

Chapter 12, Figure 2. Localization of phot1-green fluorescent protein (GFP) in guard cells and leaf epidermal cells. Red fluorescence is from chloroplasts. See Sakamoto and Briggs (2002).