PHOTOMORPHOGENESIS IN PLANTS
AND BACTERIA
3RD EDITION
Photomorphogenesis in Plants and Bacteria
3rd Edition
Function and Signal Transduction Mechanisms

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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.

REFERENCES


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<tr>
<td>AFLP</td>
<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>
<td>bilin-binding pocket</td>
</tr>
<tr>
<td>Bch</td>
<td>bacteriochlorophyll</td>
</tr>
<tr>
<td>BHF</td>
<td>blue light high fluence</td>
</tr>
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HKRD  histidine kinase-related domain  
HO    heme oxygenase  
HPT   histidine phosphotransferase  
HWE   His/Try/Asp  
HY5   hypocotyl 5  
ICGs  interchromatin granular clusters  
LFR   low Fluence Response  
LHCB  light harvesting chlorophyll a/b-binding protein  
LHY   late elongated hypocotyl  
LIA   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-Protochlorophyrin IX monomethyl ester  
MS    mass Spectroscopic analysis  
MTHF  methenyltetrahydrofolate  
NAI2  nitrate reductase  
NDPK2 nucleotide 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/Arnt/Sim  
PCB   3(Z)-phycocyanobilin  
Pchlide  protochlorophyllide  
Peb   phycoerythrobilin  
PER   period  
PFT1  phytochrome flowering time 1  
Ply   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  
PФB  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
ROS reactive oxygen species
RR response regulator
Rubisco ribulose-1,5-bisphosphate carboxylase/oxygenase
SAP sequestered areas of phytochrome
SCF complex Skp1 cullin F-box protein
SCN suprachiasmatic nucleus
SOC1 suppressor of overexpression of co 1
SPA1 suppressor of phyA 1
SPY spindly
SRD serine-rich domain
SRR1 sensitivity to red light reduced
TC-HK two-component histidine kinase
TIC time for coffee
TIM timeless
TIR3 toll interleukin resistance domain containing protein
toc1 timing of cab expression 1
ULI UV-B light insensitive
ULI3 UV-B light insensitive 3
UV ultra violet light
UV-A 320-400 nm UV
UV-B 280-320 nm UV
UV-C <280 nm UV
VLFR very low fluence response
ZT zeitgeber time
ZTL zeitlupe
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).