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

Edited by

EBERHARD SCHÄFER
Albert-Ludwig-Universität Freiburg, Germany
and
FERENC NAGY
Institute of Plant Biology, Szeged, Hungary

Springer
This book is dedicated to

Hans Mohr,

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

on the occasion of his 75\textsuperscript{th} anniversary (May 11\textsuperscript{th} 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


E. Schäfer¹ and F. Nagy²

¹University of Freiburg
Institute of Biology II/ Botany
Schänzlestr. 1
D-79104 Freiburg
Germany
Eberhard.Schaefer@biologie.uni-freiburg.de

²Biological Research Center
Institute of Plant Biology
P. O. Box 521
H-6701 Szeged
Hungary
nagyf@nucleus.szbk.u.szeged.hu
PART 1: GENERAL INTRODUCTION AND HISTORICAL OVERVIEW OF PHOTOMORPHOGENESIS

Chapter 1
HISTORICAL OVERVIEW
Eberhard Schäfer and Ferenc Nagy

1. Introduction ................................................................. 1
2. Phytochrome Induction Responses .................................... 2
3. The “High Irradiance Responses” .................................... 8
4. Very Low Fluence Responses .......................................... 10
5. Further reading ........................................................ 10
6. References .............................................................. 10

Chapter 2
PHYSIOLOGICAL BASIS OF PHOTOMORPHOGENESIS
Eberhard Schäfer and Ferenc Nagy

1. Introduction ................................................................. 13
2. Classical action spectroscopy .......................................... 13
3. Mode of function of phytochrome .................................... 16
4. Correlations between in vivo spectroscopical measurements and physiological responses ........................................ 18
5. Phytochrome response types .......................................... 20
6. Summary .................................................................. 21
8. References .............................................................. 22

Chapter 3
HISTORICAL OVERVIEW OF MOLECULAR BIOLOGY AND GENETICS IN PHOTOMORPHOGENESIS
Eberhard Schäfer and Ferenc Nagy

References ........................................................................ 30
Chapter 4

GENETIC BASIS AND MOLECULAR MECHANISMS OF SIGNAL TRANSDUCTION FOR PHOTOMORPHOGENESIS

Eberhard Schäfer and Ferenc Nagy

1. Introduction ........................................................................... 33
2. Phototropism mutants .......................................................... 34
3. Photomorphogenic mutants .................................................... 34
4. Circadian mutants .................................................................. 35
5. Genetic variation, mutants identified by QTL mapping ............ 35
6. Signal transduction mutants ................................................... 36
7. Signal transduction at the molecular level .............................. 37
8. Summary .............................................................................. 38
9. References ............................................................................ 39

PART 2: THE PHYTOCHROME

Chapter 5

THE PHYTOCHROME CHROMOPHORE

Seth J. Davis

1. Introduction ........................................................................... 41
2. Structure of the phytochrome chromophore ............................ 44
3. Phytochromobilin synthesis .................................................... 47
   3.1 Heme Oxygenases ............................................................ 50
   3.2 Phytochromobilin Synthase ............................................... 53
4. Holo assembly ....................................................................... 55
5. Biophysics of the chromophore .............................................. 58
6. Personal Perspectives ............................................................ 59
   6.1 Phy chromophore structure ............................................... 59
   6.2 Phy chromophore synthesis .............................................. 59
   6.3 Holo-phy assembly and structure ..................................... 59
7. References ............................................................................ 60
Chapter 6

STRUCTURE, FUNCTION, AND EVOLUTION OF MICROBIAL PHYTOCHROMES
Baruch Karniol and Richard D. Vierstra

1. Introduction ........................................................................................................... 65
2. Higher plant phys ............................................................................................... 66
3. The Discovery of microbial Phys ..................................................................... 69
4. Phylogeny of the Phy Superfamily .................................................................... 72
   4.1 Cyanobacterial phy (Cph) family .................................................................. 76
   4.2 Bacteriophytochrome (BphP) family .......................................................... 76
   4.3 Fungal phy (Fph) family .............................................................................. 83
   4.4 Phy-like sequences ...................................................................................... 84
5. Downstream signal transduction cascades ....................................................... 85
6. Physiological roles of microbial phys ............................................................... 88
   6.1 Directing phototaxis .................................................................................... 88
   6.2 Enhancement of photosynthetic potential .................................................. 89
   6.3 Photocontrol of pigmentation ...................................................................... 91
7. Evolution of the phy superfamily ..................................................................... 92
8. Perspectives ........................................................................................................ 94
9. References .......................................................................................................... 95

Chapter 7

PHYTOCHROME GENES IN HIGHER PLANTS: STRUCTURE, EXPRESSION, AND EVOLUTION
Robert A. Sharrock and Sarah Mathews

1. Introduction ......................................................................................................... 99
2. Phytochrome gene structures and protein sequences ....................................... 100
   2.1 The first phytochrome sequences ................................................................ 100
   2.2 Phytochrome is a family of related photoreceptors encoded by multiple PHY genes in higher plants ......................................................... 101
   2.3 Phytochrome nomenclature ....................................................................... 105
   2.4 Heterodimerization of type II phytochromes .............................................. 105
3. Expression patterns of phytochromes in plants ............................................... 106
   3.1 How important are phytochrome expression patterns? ......................... 106
   3.2 Assaying phytochromes ............................................................................. 107
   3.3 Early Expression Studies ........................................................................... 107
   3.4 Patterns of PHY gene expression – mRNA levels and promoter fusion experiments ................................................................................. 108
   3.5 The levels and distributions of phytochromes in plants ............................ 112
PART 3: BLUE-LIGHT AND UV-RECEPTORS

Chapter 10
BLUE/UV-A RECEPTORS: HISTORICAL OVERVIEW
Winslow R. Briggs

1. Introduction................................................................. 171
2. Early history.............................................................. 172
3. Phototropism: action spectra can be fickle......................... 174
4. The LIAC: a frustrating digression................................ 179
5. The cryptochrome story................................................. 180
6. The phototropin story.................................................... 182
7. Stomatal opening in blue light........................................ 184
8. Chloroplast movements induced by blue light..................... 186
9. Leaf expansion............................................................ 187
10. The rapid inhibition of growth....................................... 189
11. Solar tracking............................................................ 191
12. The ZTL/ADO family................................................... 191
13. Conclusions.............................................................. 191
14 References..................................................................... 192

Chapter 11
CRYPTOCHROMES
Anthony R. Cashmore

1. Introduction................................................................. 199
2. Photolyases................................................................. 199
3. The discovery of cryptochrome......................................... 200
   3.1 Cryptochromes of Arabidopsis..................................... 201
   3.2 Cryptochromes of algae, mosses and ferns..................... 202
   3.3 Drosophila cryptochrome.......................................... 202
   3.4 Mammalian cryptochromes....................................... 203
   3.5 Bacterial and related cryptochromes............................ 203
4. Cryptochromes and plant photomorphogenesis.................... 203
5. Cryptochrome and flowering .......................................................... 206
6. Plant cryptochromes and circadian rhythms ................................. 206
7. Arabidopsis cryptochrome and gene expression ......................... 207
8. Cryptochromes and circadian rhythms in animals ....................... 208
   8.1 Drosophila circadian rhythms are entrained through cryptochrome.. 208
   8.2 Mammalian cryptochromes: Negative transcriptional regulators and essential components of the circadian oscillator .... 208
9. The mode of action of cryptochrome ............................................ 210
   9.1 The Arabidopsis cryptochrome C-terminal domain mediates a constitutive light response ......................................................... 210
   9.2 COP1: A signalling partner of Arabidopsis cryptochromes ......... 211
   9.3 Intracellular localization of Arabidopsis CRYs ........................ 213
   9.4 Phosphorylation of Arabidopsis cryptochromes ....................... 214
   9.5 Photochemical properties of Arabidopsis cryptochromes ......... 215
   9.6 Drosophila cryptochrome interacts with PER and TIM in a light-dependent manner ................................................................. 216
   9.7 Mouse cryptochromes negatively regulate transcription in a light-independent manner ............................................................. 217
10. Cryptochrome evolution ........................................................... 217
11. Conclusions and future studies ................................................. 217
12. References .................................................................................... 218

Chapter 12

PHOTOTROPINS
Winslow R. Briggs, John M. Christie and Trevor E. Swartz

1. Introduction ..................................................................................... 223
2. Blue light-activated phosphorylation of a plasma-membrane protein ......................................................... 224
   2.1 The protein is likely ubiquitous in higher plants .................... 224
   2.2 Subcellular localization of phot1 ............................................. 225
   2.3 Distribution of the phototropins in relation to function .......... 226
   2.4 Biochemical properties of the phosphorylation reaction in vitro ............................................................... 227
   2.5 Correlation of phot1 phosphorylation with phototropism ....... 228
   2.6 Autophosphorylation occurs on multiple sites ....................... 231
3. Cloning and molecular characterization of phototropin ................. 232
   3.1 The initial discovery of phototropin 1 ................................. 232
   3.2 LOV domains function as light sensors ............................... 234
4. Why two LOV domains? ............................................................... 234
5. Structural and photochemical properties of the LOV domains ....... 236
   5.1 LOV domain photochemistry ............................................. 236
   5.2 LOV-domain structure ....................................................... 236
   5.3 The LOV-domain photocycle ............................................. 238
   5.4 Mechanism of FMN-cysteiny1 adduct formation ................... 238
Chapter 13

BLUE LIGHT PHOTORECEPTORS - BEYOND PHOTOTROPINS AND CRYPTOCHROMES
Jay Dunlap

1. Introduction.......................................................... 253
2. Historical antecedents............................................... 253
3. The photobiology of Neurospora......................................... 255
4. Light perception - the nature of the blue light photoreceptor......... 257
   4.1 Flavins as chromophores........................................ 257
   4.2 Genetic dissection of the blue light response.................. 257
5. Cloning of the white collar genes..................................... 258
6. WHITE COLLAR-1 is the blue light photoreceptor.................. 260
7. WC-1 and WC-2 - positive elements in the circadian feedback loop..... 263
   7.1 How light resets the clock..................................... 265
8. VIVID, a second photoreceptor that modulates light responses.......... 266
9. Complexities in light regulatory pathways................................ 268
10. Other Neurospora photoreceptors..................................... 270
11. Flavin binding domain proteins as photoreceptors in photosynthetic eukaryotes..................................................... 271
12. Summary and conclusion............................................ 273
13. References.......................................................... 274

Chapter 14

UV-B PERCEPTION AND SIGNALLING IN HIGHER PLANTS
Roman Ulm

1. Introduction.......................................................... 279
2. DNA damage and repair................................................ 281
3. Photomorphogenic responses to UV-B................................... 284
   3.1 Synthesis of “sunscreen” metabolites............................. 285
   3.2 Inhibition of hypocotyl growth.................................... 287
   3.3 Cotyledon opening and expansion.................................. 288
4. UV-B perception............................................................... 289
   4.1 Supporting evidence and possible nature of a specific UV-B
       photoreceptor.......................................................... 289
   4.2 Possible importance of specific UV-B perception?............ 291
5. UV-B signalling............................................................. 292
   5.1 Reactive oxygen species............................................. 292
   5.2 Plant hormones....................................................... 293
   5.3 Calcium................................................................. 294
   5.4 Phosphorylation....................................................... 294
   5.5 Nitric oxide............................................................ 295
6. Transcriptional response to UV-B radiation........................ 296
7. Conclusions and perspectives.......................................... 298
8. References.......................................................................... 299

Chapter 15

SIGNAL TRANSDUCTION IN BLUE LIGHT-MEDIATED RESPONSES
Vera Quecini and Emmanuel Liscum

1. Introduction................................................................. 305
2. Cryptochrome signalling................................................ 305
   2.1 Cryptochromes and photomorphogenesis....................... 305
      2.1.1 Cryptochrome signalling and photomorphogenic growth
            responses............................................................ 306
      2.1.2 Cryptochrome signalling and electrophysiological processes
            ................................................................. 309
      2.1.3 Cryptochrome signalling and the regulation of gene
            expression.......................................................... 311
3. Phototropin signalling.................................................... 311
   3.1 Phototropins and plant movement responses................... 311
      3.1.1 Phototropins and phototropism............................... 312
      3.1.2 Phototropins and stomatal aperture control................ 316
      3.1.3 Phototropins and chloroplast movement..................... 318
   3.2 Phototropin signalling and electrophysiological processes... 320
4. Concluding remarks....................................................... 321
5. References.......................................................................... 321
PART 4: SIGNAL TRANSDUCTION IN PHOTOMORPHOGENESIS

Chapter 16

GENERAL INTRODUCTION
Peter H. Quail

References........................................................................................................ 333

Chapter 17

PHYTOCHROME SIGNAL TRANSDUCTION NETWORK
Peter H. Quail

1. Introduction.............................................................................................. 335
2. Genetically-identified signalling-intermediate candidates....................... 337
3. Phytochrome-Interacting Factors.............................................................. 340
   3.1 PIF3................................................................................................ 340
   3.2 PKS1............................................................................................. 343
   3.3 NDPK2........................................................................................... 344
   3.4 Other phy interactors.................................................................... 344
4. Transcription-factor genes are early targets of PHY signalling............ 345
5. Biochemical mechanism of signal transfer.......................................... 353
6. References............................................................................................. 354

Chapter 18

THE FUNCTION OF THE COP/DET/FUS PROTEINS IN CONTROLLING PHOTOMORPHOGENESIS: A ROLE FOR REGULATED PROTEOLYSIS
Elizabeth Strickland, Vicente Rubio and Xing Wang Deng

1. Introduction................................................................................................ 357
   1.1 Genetic analysis of photomorphogenesis...................................... 357
2. A brief summary of the ubiquitin-proteasome system............................ 359
3. Properties and functions of the pleiotropic COP/DET/FUS proteins.... 359
   3.1 COP1................................................................................................. 359
      3.1.1 Nuclear localization of COP1.............................................. 360
      3.1.2 Light regulation of COP1..................................................... 360
      3.1.3 Molecular role of COP1......................................................... 361
      3.1.4 The E3 ubiquitin-protein ligase activity of COP1.......... 363
      3.1.5 COP1 interactors................................................................. 364

2. Photoreceptor interaction during de-etiolation
   2.1 Multiple photoreceptors control de-etiolation
   2.2 Redundancy
      2.2.1 The potential action of a photoreceptor can be hidden by the action of others
      2.2.2 Definition of redundancy
      2.2.3 The mechanisms of redundancy
      2.2.4 Redundant photoreceptors are not equally important
   2.3 Synergism between phytochromes and cryptochromes
      2.3.1 Blue light-mediated responsivity amplification towards phytochrome
      2.3.2 cry1 amplifies responsivity towards phyB
      2.3.3 The synergism between cry1 and phyB is conditional
      2.3.4 Other manifestations of synergism between phytochromes and cryptochromes
   2.4 Synergistic or antagonistic interaction between phyA and phyB
   2.5 Synergism between phyB and phyC
   2.6 Interactive signalling under sunlight reduces noise/signal ratio
3. Photoreceptor interaction during adult plant body shape formation
   3.1 Redundant control of normal progression of vegetative development by phytochromes and cryptochromes
   3.2 The response to R:FR
4. Photoreceptor interaction in phototropism
   4.1 Phototropins perceive the unilateral stimulus
   4.2 Phytochromes enhance the responses mediated by phototropins
   4.3 The role of cryptochromes
5. Photoreceptor interaction in clock entrainment
6. Photoreceptor interaction controlling flowering
   6.1 Different light signals control the transition between vegetative and reproductive growth
   6.2 Roles of cry2, cry1, and phyA in the photoperiodic response
   6.3 Roles of phyB, phyD, and phyE in the response to low R:FR
   6.4 Integration of the responses to photoperiod and R:FR
7. Points of convergence in the photoreceptor signalling network
   7.1 The occurrence of interactions is an emergent property of the signalling network
   7.2 Direct convergence: Physical interaction between photoreceptor pigments
   7.3 Convergence in the control of transcription: HFR1
   7.4 Post-transcriptional convergence accounts for the interaction between phyB and phyC
   7.5 Convergence in the control of protein stability: COP1
   7.6 Photoreceptor sub-cellular partitioning
   7.7 SUB1
8. Overview
Chapter 21
INTERACTION OF LIGHT AND HORMONE SIGNALLING TO MEDIATE
PHOTOMORPHOGENESIS
Michael M. Neff, Ian H. Street, Edward M. Turk and Jason M. Ward

1. Introduction................................................................................................... 439
2. Gibberellins................................................................................................... 440
   2.1 Gibberellin biosynthetic genes and seed germination......................... 440
   2.2 Gibberellins and de-etiolation............................................................. 442
   2.3 The SPY and PHOR1 genes................................................................. 443
   2.4 A possible role for protein degradation............................................... 444
   2.5 Interactions with other hormone signalling pathways....................... 445
3. Auxin............................................................................................................ 446
   3.1 Auxin transport................................................................................... 447
   3.2 Auxin and phototropism..................................................................... 448
   3.3 Auxin and shade avoidance............................................................... 449
   3.4 Auxin responsive genes involved in photomorphogenesis.................. 450
   3.5 Auxin and protein degradation.......................................................... 451
   3.6 Interaction of auxin with other hormone signalling pathways............ 452
4. Brassinosteroids............................................................................................ 452
   4.1 Brassinosteroid-deficient mutants...................................................... 454
   4.2 Brassinosteroids and gene expression............................................... 455
   4.3 Further genetic connections between brassinosteroids and light........ 455
   4.4 Brassinosteroids and light signalling: three speculative models........ 456
5. Ethylene........................................................................................................ 460
   5.1 Genetic connections between ethylene and photomorphogenesis....... 461
   5.2 Ethylene mutants and shade-avoidance.......................................... 462
   5.3 Ethylene and fruit ripening............................................................... 463
6. Cytokinins.................................................................................................. 463
7. Summary..................................................................................................... 465
8. Further reading............................................................................................ 465
9. References.................................................................................................... 466
PART 5: SELECTED TOPICS

Chapter 22

THE ROLES OF PHYTOCHROMES IN ADULT PLANTS
Keara A. Franklin and Garry C. Whitelam

1. Introduction............................................................................................... 475
2. The natural light environment................................................................. 477
3. R:FR ratio and shade avoidance......................................................... 478
4. Roles of different phytochromes in shade avoidance............................. 482
   4.1 Roles for phytochrome A in adult plants........................................ 486
5. Molecular mechanisms controlling shade avoidance responses............. 489
   5.1 The acceleration of flowering....................................................... 489
   5.2 Early events in R:FR ratio signalling............................................. 491
6. References............................................................................................... 493

Chapter 23

A ROLE FOR CHLOROPHYLL PRECURSORS IN PLASTID-TO-NUCLEUS SIGNALING
Robert M. Larkin and Joanne Chory

1. Introduction.............................................................................................. 499
2. Chlorophyll biosynthetic mutant, inhibitor, and feeding studies.......... 500
3. Plastid-to-nucleus signaling mutants inhibit Mg-porphyrin accumulation. 504
4. Mechanism of Mg-Proto/Mg-ProtoMe signaling.................................. 506
5. Plastid and light signaling pathways appear to interact....................... 508
6. Conclusions and perspectives............................................................... 509
7. Further Reading..................................................................................... 510
8. References.............................................................................................. 510

Chapter 24

PHOTOMORPHOGENESIS OF FERNS
Takeishi Kanegae and Masamitsu Wada

1. Introduction.............................................................................................. 515
2. Photoreceptors in Adiantum................................................................. 517
   2.1 Cryptochromes................................................................................. 517
   2.2 Phototropins.................................................................................. 518
   2.3 Phytochromes............................................................................... 519
THE MOLECULAR GENETICS OF PHOTO-PERIODIC RESPONSES: COMPARISONS BETWEEN LONG-DAY AND SHORT-DAY SPECIES
George Coupland

Chapter 28
COMMERCIAL APPLICATIONS OF PHOTOMORPHOGENESIS RESEARCH
Ganga Rao Davuluri and Chris Bowler

Chapter 29
PHOTOMORPHOGENESIS – WHERE NOW?
Harry Smith
Abbreviations

AFLP amplified fragment-length polymorphism
APRR Arabidopsis pseudo response regulator
ATP adenosine triphosphate
B blue light
BBP bilin-binding pocket
Bch bacteriochlorophyll
BHF blue light high fluence
BLF blue light low fluence
BphPs bacteriophytochrome photoreceptors
BV biliverdin IXα
CAB chlorophyll a/b binding proteins
CAT3 catalase 3
CCA complementary chromatic adaptation
CCAl circadian clock-associated 1
CCR2 cold circadian clock-regulated
CCT cryptochrome C-terminal domain
CFB cytophaga-flexibacter-bacterioides
Chl chloroplast
CHS chalcone synthase
CNT cryptochrome N-terminal domain
CO constans
COP1 constitutively photomorphogenic 1
CPD cyclobutane pyrimidine dimmers
Cphs cyanobacterial Phys
Crt carotenoids
CRY cryptochrome
Cryl/ hy4 cryptochrome1/ hypocotyl4
CT circadian Time"
Cyto cytoplasm
DBD DNA-binding domain
DDB1 UV-damaged DNA binding protein
DET1 de-etiolated 1
DET2 de-etiolated 2
DUF domain of unknown function
ELF3 early flowering 3
ELF4 early-Flowering 4
EPR1 early phytochrome responsive 1
FAD flavin adenine dinucleotide
FDD fluorescence differential display
FKF1 flavin-binding kelch repeat F-box 1
FLC flowering locus C
Fphs fungal Phys
FR far-red
FSBA fluorosulfonylbenzoyladenosine
FT flowering locus T
G green light
GA gibberelin acid
GAF cGMP phosphodiesterase/adenyl cyclase/FhlA
GAI GA-insensitive
GFP green fluorescent protein
GGDEF Gly/Gly/Asp/Gly/Phe motif
GI gigantea
GRAS GAI/RGA and SCARECROW
HAMP HK/adenyl cyclases/methyl-l-binding proteins/phophatases domain
Hd heading date
HIR high irradiance response
HKD histidine kinase domain
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
LIAc 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 methylene/tetrahydrofolate
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
PIF1  PIF3-like 1
PIF2  PIF3-like 2
PIF4  PIF3-like 4
PIF6  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
<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<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>
</tr>
<tr>
<td>SCF complex</td>
<td>Skp1 cullin F-box protein</td>
</tr>
<tr>
<td>SCN</td>
<td>suprachiasmatic nucleus</td>
</tr>
<tr>
<td>SOC1</td>
<td>suppressor of overexpression of co1</td>
</tr>
<tr>
<td>SPA1</td>
<td>suppressor of phyA1</td>
</tr>
<tr>
<td>SPY</td>
<td>spindly</td>
</tr>
<tr>
<td>SRD</td>
<td>serine-rich domain</td>
</tr>
<tr>
<td>SRR1</td>
<td>sensitivity to red light reduced</td>
</tr>
<tr>
<td>TC-HK</td>
<td>two-component histidine kinase</td>
</tr>
<tr>
<td>TIC</td>
<td>time for coffee</td>
</tr>
<tr>
<td>TIM</td>
<td>timeless</td>
</tr>
<tr>
<td>TIR3</td>
<td>toll interleukin resistance domain containing protein</td>
</tr>
<tr>
<td>toc1</td>
<td>timing of cab expression1</td>
</tr>
<tr>
<td>ULI</td>
<td>UV-B light insensitive</td>
</tr>
<tr>
<td>ULI3</td>
<td>UV-B light insensitive3</td>
</tr>
<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>
</tr>
<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>
</tr>
</tbody>
</table>
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).