

Contents

Contributors	xiii
Preface	xv
Part I Photoreceptors	1
1 Phytochromes	3
ANDREAS HILTBRUNNER, FERENC NAGY AND EBERHARD SCHÄFER	
1.1 Introduction	3
1.2 Historical aspects	3
1.3 Properties of phyA <i>in vivo</i>	4
1.4 Properties in yeast cells	4
1.5 <i>In vivo</i> properties of phytochromes	5
1.5.1 <i>In vivo</i> spectroscopy	5
1.6 Intracellular localisation of phytochromes	7
1.6.1 Classical methods	7
1.6.2 Spectroscopic methods	7
1.6.3 Cell biological methods	8
1.6.4 Immunocytochemical methods	8
1.6.5 Novel methods	8
1.7 Intracellular localisation of phyB in dark and light	9
1.8 Intracellular localisation of phyA in dark and light	11
1.9 Intracellular localisation of phyC, phyD and phyE in dark and light	12
1.10 Phytochrome/PIF3 co-localisation and nuclear speckles	12
1.11 Regulation of intracellular localisation of phytochromes	13
Acknowledgements	14
References	15
2 Cryptochromes	17
ALFRED BATSCHAUER, ROOPA BANERJEE AND RICHARD POKORNY	
2.1 Introduction	17
2.2 Cryptochrome genes and their evolution	17
2.3 Cryptochrome domains, chromophores and structure	20
2.3.1 Domain structure of the cryptochromes	20
2.3.2 Cryptochrome chromophores	21

2.3.3	Photolyase and cryptochrome structure	22
2.3.3.1	Photolyase structure and reaction mechanism	22
2.3.3.2	Cryptochrome structure	23
2.4	Cryptochrome biochemistry and spectroscopy	25
2.4.1	Phosphorylation	25
2.4.2	Nucleotide-binding and kinase activity	25
2.4.3	DNA-binding activity	26
2.4.4	Electron transfer	27
2.5	Expression and biological activity of cryptochromes	28
2.5.1	Expression and light regulation of cryptochromes in planta	28
2.5.2	Cellular localization	31
2.5.3	Growth responses controlled by cryptochromes	31
2.5.4	Regulation of gene expression through cryptochromes	33
2.6	Cryptochrome signalling	35
2.6.1	Dimerization and output domains	36
2.6.2	Cryptochrome partners	38
2.6.2.1	Interaction with COP1	39
2.6.2.2	Interaction with zeittupe/ADAGIO1	39
2.6.2.3	Interaction with phytochromes	40
2.6.3	Further downstream components	41
2.7	Summary	43
	Acknowledgements	43
	References	43
3	Phototropins and other LOV-containing proteins	49
	JOHN M. CHRISTIE	
3.1	Introduction	49
3.2	Phototropins and their biological functions	50
3.2.1	Physiological roles in higher plants	50
3.2.2	Physiological roles in lower plants	52
3.3	Phototropin structure, localization and activity	53
3.3.1	Phototropin structure and localization	53
3.3.2	Phototropin autophosphorylation	55
3.4	Light sensing by the LOV domains	57
3.4.1	LOV-domain photochemistry	57
3.4.2	LOV-domain structure	59
3.4.3	Functional roles of LOV1 and LOV2	60
3.4.4	Light-induced protein movements	62
3.5	Phototropin signaling	63
3.5.1	Phototropin-interacting proteins	63
3.5.2	Downstream signaling-targets	65
3.6	Other LOV-containing proteins	67
3.6.1	LOV-containing proteins in Arabidopsis	67
3.6.2	LOV-containing proteins in fungi	70
3.6.3	LOV-containing proteins in bacteria	72

3.7	Conclusions and future perspectives	73
	Acknowledgements	73
	References	74
Part II	Photoreceptor signal transduction	79
4	Phytochrome-interacting factors	81
	PETER H. QUAIL	
4.1	Introduction	81
4.2	Methodology	81
4.2.1	Initial identification of PIFs	81
4.2.2	Subsequent assay and characterization of the interaction	82
4.2.3	Reverse genetic assessment of functional relevance to phy signalling	83
4.3	phy-interactors	84
4.3.1	PIF3	84
4.3.2	Other bHLH transcription factors and the active phyB binding domain	90
4.3.3	Nucleoside diphosphate kinase 2	93
4.3.4	Phytochrome kinase substrate 1	94
4.3.5	Type 5 protein phosphatase	94
4.3.6	Protein phosphatase 2A	95
4.3.7	Early flowering 3	95
4.3.8	Far-red elongated hypocotyl 1	96
4.4	Pre-selected interaction targets	96
4.4.1	<i>Arabidopsis</i> response regulator 4	96
4.4.2	Zeitlupe	97
4.4.3	Cryptochrome 1 and 2	97
4.4.4	AUX/IAA proteins	98
4.4.5	COP1	98
4.5	Perspective	99
	Acknowledgements	100
	References	101
5	Phosphorylation/dephosphorylation in photoreceptor signalling	106
	CATHERINE LILLO, TRUDIE ALLEN AND SIMON GEIR MØLLER	
5.1	Introduction	106
5.1.1	The photoreceptors autophosphorylate, but the classical activation loop is not involved	107
5.1.2	Phosphatases in photoreceptor signalling	108
5.2	Phytochromes	109
5.2.1	Phosphorylation of phytochrome	109
5.2.2	Phytochrome kinase substrate 1	110
5.2.3	Nucleoside diphosphate kinase 2	111

5.2.4	FYPP	112
5.2.5	PAPP5	113
5.3	Cryptochromes	114
5.3.1	Cryptochrome phosphorylation	114
5.3.2	Phosphorylation of the C-terminal end is necessary for signal transduction	115
5.4	Phototropins	116
5.5	Is phosphorylation/dephosphorylation important for downstream events?	118
5.5.1	HY5	118
5.5.2	Long hypocotyl in far-red light	119
5.5.3	Circadian clock-associated and late elongated hypocotyl	119
5.5.4	EID1	120
5.5.5	Aux/IAA	120
5.5.6	PP7	121
5.5.7	Downstream of phototropin	121
5.6	Conclusions	122
	References	123

6 The role of ubiquitin/proteasome-mediated proteolysis in photoreceptor action 128

SUHUA FENG AND XING WANG DENG

6.1	Introduction	128
6.2	Overview of the ubiquitin/proteasome system	129
6.2.1	Ubiquitin conjugation and deconjugation pathways	129
6.2.2	Diversity of E3 Ub ligases	130
6.2.3	26S proteasome	131
6.3	Role of COP/DET/FUS proteins in photoreceptor-mediated signal transduction and ubiquitin/proteasome-mediated proteolysis	132
6.3.1	COP/DET/FUS proteins integrate divergent photoreceptor signaling pathways and downstream gene expression	132
6.3.2	COP1	134
6.3.2.1	Light regulation of COP1 localization	135
6.3.2.2	COP1 acts as an E3 Ub ligase	136
6.3.2.3	Interaction between photoreceptors and COP1	137
6.3.3	CDD complex	137
6.3.3.1	COP10 is an E2 Ub-conjugating enzyme variant	137
6.3.3.2	COP10 forms a complex with DET1 and DDB1	138
6.3.4	COP9 signalosome	139
6.3.4.1	Composition and structure of the COP9 signalosome	139

6.3.4.2	Biochemical activities of the COP9 signalosome	140
6.3.4.3	Regulation of cullin-containing E3 Ub ligases by the COP9 signalosome	140
6.3.5	SPA protein family	142
6.4	Other connection points between light signaling and selective proteolysis	143
6.4.1	F-box proteins that are involved in light signaling	143
6.4.2	Other light signaling pathway components that are targets of proteolysis	144
6.4.2.1	Phytochrome A	144
6.4.2.2	Cryptochrome 2	144
6.4.2.3	Phytochrome-interacting factor 3 and far-red elongated hypocotyl 1	145
6.5	Concluding remarks	146
	References	147
7	UV-B perception and signal transduction	155
	GARETH I. JENKINS AND BOBBY A. BROWN	
7.1	Introduction	155
7.2	UV-B in the environment	156
7.3	Plant responses to UV-B	157
7.4	UV-B perception and signal transduction	159
7.4.1	Non-photomorphogenic UV-B signalling	160
7.4.1.1	Damage/stress signalling	160
7.4.1.2	Overlap with defence/wound signalling	162
7.4.2	Photomorphogenic UV-B signalling	163
7.4.2.1	UV-B perception	164
7.4.2.2	Signal transduction	166
7.5	Genetic approach	167
7.5.1	Screens for UV-B signalling mutants	167
7.5.2	UVR8	170
7.5.3	HY5	173
7.5.4	Other transcription factors involved in UV-B responses	174
7.6	Concluding remarks	175
	Acknowledgements	176
	References	176
Part III	Physiological responses	183
8	Photocontrol of flowering	185
	PAUL DEVLIN	
8.1	Introduction	185
8.2	Internal cues	187
8.2.1	The autonomous pathway	187
8.2.2	The gibberellin-dependent pathway	189

8.3	External cues	189
8.3.1	Photoperiodism	189
8.3.1.1	Long days or short nights?	190
8.3.1.2	The circadian clock	191
8.3.1.3	The coincidence model	196
8.3.1.4	Flowering time mutants of <i>Arabidopsis</i>	197
8.3.1.5	Application to other species	199
8.3.1.6	Site of perception of photoperiodic stimulus	200
8.3.2	Shade avoidance	201
8.3.3	Vernalisation	203
8.4	Convergence of the flowering pathways	203
8.5	Conclusion	205
	References	205
9	Red:far-red ratio perception and shade avoidance	211
	KEARA A. FRANKLIN AND GARRY C. WHITE LAM	
9.1	Introduction	211
9.2	Natural light environment	211
9.3	Shade avoidance syndrome	215
9.4	Phytochrome regulation of shade avoidance	217
9.4.1	The role of phytochromes B, D and E in R:FR ratio signalling	218
9.4.2	The role of phyA in R:FR ratio signalling	220
9.5	The roles of other signals in shade avoidance	221
9.5.1	PAR and B signals	221
9.5.2	Hormone signals	222
9.6	Signalling in shade avoidance	224
9.6.1	<i>ATHB-2</i>	224
9.6.2	<i>PIL1</i>	224
9.6.3	R:FR ratio and flowering	226
9.7	The adaptive value of shade avoidance	227
9.8	Conclusions	228
	References	229
10	Photoreceptor interactions with other signals	235
	EVE-MARIE JOSSE AND KAREN J. HALLIDAY	
10.1	Introduction	235
10.2	Light-clock connections	235
10.2.1	The clock	235
10.2.2	Photoentrainment	237
10.2.3	Light control of flowering time	239
10.3	Light-hormone connections	240

10.4	Light and auxin signal integration	240
10.4.1	Light regulation of auxin biosynthesis and transport	241
10.4.2	Signalling components shared by light and auxin	242
10.4.2.1	Light regulation of the <i>GH3</i> gene family	242
10.4.2.2	Role of Aux/IAs and proteolysis in light and auxin signalling	243
10.5	The tropisms	244
10.5.1	Light and auxin control of shoot phototropism	245
10.5.2	Phytochrome and cryptochrome modification of shoot phototropism	246
10.5.3	Root phototropism	247
10.5.4	Gravitropism	247
10.5.5	Light regulation of gravitropism	248
10.6	Light and GA signal integration	249
10.6.1	Phytochrome regulation of GA biosynthesis and homeostasis	249
10.6.2	Light regulation of GA signalling	250
10.7	The thermosensory pathways	251
10.8	Summary	255
	References	256
Part IV	Applied aspects of photomorphogenesis	265
11	Photoreceptor biotechnology	267
	MATTHEW HUDSON	
11.1	Introduction and background	267
11.2	Approaches to modification of photomorphogenic responses in crop plants	268
11.2.1	Dwarfing plants using photoreceptors	268
11.2.2	The shade-avoidance response	269
11.2.2.1	Control of gene expression and shade avoidance	270
11.2.2.2	Alteration of the timing of flowering	271
11.2.2.3	Taxonomic differences and similarities in higher plants	272
11.3	Modification of photomorphogenesis using genetic transformation – the state of the art	273
11.3.1	Plants transgenic for phytochromes	273
11.3.2	Modification of other photoreceptors	276
11.3.3	Overexpression of signaling components	278
11.4	Modification of photomorphogenesis by utilizing genetic diversity	278
11.4.1	Natural variation in photomorphogenesis	278
11.4.2	Photoreceptors and photomorphogenic genes as targets for selection in crops	280

11.5	Photoreceptor biotechnology <i>ex planta</i>	281
11.5.1	Using phytochrome to control gene expression	281
11.5.2	Phytochromes as fluorescent probes	282
11.5.3	Other potential uses of photoreceptors	284
11.6	Future directions in photoreceptor biotechnology	284
	Acknowledgements	285
	References	285
12	Light-quality manipulation by horticulture industry	290
	NIHAL C. RAJAPAKSE AND YOSEPHA SHAHAK	
12.1	Introduction	290
12.2	Regions of light spectrum important for plant growth and development	290
12.3	Plant responses to quality of light	292
12.4	Light manipulation by horticulture industry	293
12.4.1	Electric light sources	294
12.4.2	Spectral filters	295
12.4.2.1	Greenhouse covers	295
12.4.2.2	Photoselective nets	300
12.4.2.3	Coloured plastic mulch	305
12.5	Future prospects	307
	References	307
Index		313

The colour plate section follows page 30