

# CONTENTS

List of Contributors	xv
Preface	xvii
<b>1 Signal Achievements in Gibberellin Research: The Second Half-Century</b>	<b>1</b>
<i>Valerie M. Sponsel</i>	
1.1 Introduction	1
1.2 Gibberellin biosynthesis	6
1.3 Gibberellin signalling	17
1.4 Physiological responses to gibberellins	25
References	29
<b>2 Gibberellin Biosynthesis in Higher Plants</b>	<b>37</b>
<i>Peter Hedden</i>	
2.1 Introduction	37
2.2 Synthesis of <i>ent</i> -kaurene	39
2.2.1 Formation of <i>trans</i> -geranylgeranyl diphosphate	39
2.2.2 Formation of <i>ent</i> -kaurene from <i>trans</i> -geranylgeranyl diphosphate	40
2.3 Reactions catalysed by cytochrome P450 mono-oxygenases	42
2.4 Reactions catalysed by 2-oxoglutarate-dependent dioxygenases	45
2.5 Sites of gibberellin biosynthesis	49
2.6 Regulation of gibberellin biosynthesis	50
2.6.1 Developmental control	50
2.6.2 Gibberellin homeostasis	51
2.6.3 Regulation by other hormones	54
2.6.4 Regulation by environmental factors	55
2.7 Concluding remarks	59
Acknowledgements	60
References	60
<b>3 Inactivation Processes</b>	<b>73</b>
<i>Hiroshi Magome and Yuji Kamiya</i>	
3.1 Introduction	73
3.2 Gibberellin inactivation	75
3.2.1 Gibberellin 2-oxidase	75
3.2.2 Gibberellin methyltransferase	77
3.2.3 Gibberellin 16,17-oxidase	78

3.2.4	Gibberellin 13-oxidase and 12 $\alpha$ -oxidase	78
3.2.5	Conjugation with sugar	80
3.3	Regulation of gibberellin inactivation	80
3.3.1	Developmental regulation	81
3.3.2	Gibberellin homeostasis	82
3.3.3	Regulation by other hormones	83
3.3.4	Environmental regulation	84
3.4	Concluding remarks	87
	References	88
4	Gibberellin Transport	95
	<i>Jonathan Dayan</i>	
4.1	Introduction	95
4.2	Gibberellins can be translocated along plant bodies	96
4.3	Gibberellin transport in seeds	100
4.4	Pattern of gibberellin biosynthesis in transport analysis	101
4.5	Grafting experiments	103
4.6	Significance for secondary growth	104
4.7	Orientation of gibberellin signal flow: source and sink tissues	107
4.8	Monitoring intra- and intercellular gibberellin concentration	110
4.9	Conclusion: new aspects for gibberellin transport	111
4.9.1	Potential transporters	111
4.9.2	Analysis through perception	112
4.9.3	Links to sugar transport	112
	Acknowledgements	113
	References	114
5	Gibberellins in Fungi, Bacteria and Lower Plants: Biosynthesis, Function and Evolution	121
	<i>Bettina Tudzynski, Lena Studt and María Cecilia Rojas</i>	
5.1	Introduction	122
5.2	Gibberellin biosynthesis in fungi	122
5.2.1	The biosynthetic pathway in <i>F. fujikuroi</i> : genes and enzymes	122
5.2.2	Gibberellin production in distantly related fungi	126
5.2.3	Evolution of the gibberellin biosynthetic gene cluster in fungi	128
5.2.4	The role of gibberellins in plant infection	131
5.2.5	Strain improvement	132
5.3	Gibberellin biosynthesis in bacteria	133
5.3.1	Free-living rhizobacteria	133
5.3.2	Symbiotic rhizobacteria: genes and reactions of the gibberellin biosynthetic pathway	134
5.3.3	Function and evolution	137
5.4	Gibberellin biosynthesis and signalling components in lower plants	139

5.5	Concluding remarks	143
	References	144
6	Gibberellin Hormone Signal Perception: Down-Regulating DELLA Repressors of Plant Growth and Development	153
	<i>Sven K. Nelson and Camille M. Steber</i>	
6.1	Introduction	154
6.2	DELLA proteins are repressors of gibberellin responses	154
6.3	Gibberellin signalling lifts DELLA repression of gibberellin responses	157
6.4	The gibberellin receptor <i>GID1</i> ( <i>GA-INSENSITIVE DWARF1</i> )	159
6.5	The structural requirements for gibberellin binding by <i>GID1</i>	161
6.6	The structural requirements for the <i>GID1</i> -DELLA protein-protein interaction	162
6.7	The DELLA destruction model: negative regulation of DELLA repressors by <i>SLY1/GID2</i> and the ubiquitin-proteasome pathway	166
6.8	Regulation of DELLA by phosphorylation and <i>O</i> -GlcNAc modification	169
6.9	Evidence for gibberellin-independent DELLA regulation	173
6.10	Evidence for gibberellin signalling without DELLA destruction	175
6.11	Concluding remarks	177
	Acknowledgements	179
	References	179
7	DELLA Proteins: Master Regulators of Gibberellin-Responsive Growth and Development	189
	<i>Stephen G. Thomas, Miguel A. Blázquez and David Alabadí</i>	
7.1	Introduction	190
7.2	DELLAs regulate downstream gibberellin signalling	191
7.3	Gibberellins relieve DELLA-growth repression by targeting their degradation	193
7.4	Functional diversification of <i>DELLA</i> genes	194
7.5	DELLA activity invokes rapid changes in the transcriptome	197
7.6	DELLA proteins activate transcription	198
7.7	DELLAs regulate transcription by physical interaction with transcriptional regulators	199
	7.7.1 DELLAs sequester <i>bona fide</i> TFs by physical interaction	200
	7.7.2 DELLAs interact with TFs in the context of promoters	204
	7.7.3 DELLAs interact with other transcriptional regulators	206
	7.7.4 DELLAs regulate chromatin dynamics	208
7.8	A non-genomic response regulated by DELLAs	209
7.9	Analysis of DELLA protein structure-function	210

7.10	GAMYB: A transcriptional regulator of gibberellin responses during cereal grain germination and pollen development	213
7.10.1	GAMYB positively regulates gene expression in cereal aleurone cells	214
7.10.2	GAMYB regulates gibberellin-dependent anther development	216
7.11	Concluding remarks	217
	Acknowledgements	218
	References	218
8	Interactions Between Gibberellins and other Hormones	229
	<i>John J. Ross, Asemeh Miraghazadeh, Amelia H. Beckett, Laura J. Quittenden and Erin L. McAdam</i>	
8.1	Introduction	229
8.2	Interactions involving effects of other hormones on gibberellin levels	230
8.2.1	Auxin promotes gibberellin biosynthesis	230
8.2.2	Ethylene inhibits gibberellin biosynthesis	231
8.2.3	Do gibberellin and abscisic acid inhibit each other's synthesis?	232
8.2.4	Do brassinosteroids act by affecting gibberellin levels?	234
8.2.5	Possible effects of other hormones on gibberellin synthesis	234
8.3	Interactions between hormone signal transduction pathways	234
8.3.1	Do other hormones affect DELLA stability?	235
8.3.2	DELLAs interact with proteins from the signalling pathways of other hormones	237
8.4	Gibberellins and auxin transport	245
8.5	Conclusion	246
	Acknowledgements	247
	References	247
9	Gibberellins and Seed Germination	253
	<i>Terezie Urbanova and Gerhard Leubner-Metzger</i>	
9.1	Introduction	254
9.2	Spatiotemporal expression of gibberellin metabolism during Brassicaceae seed germination	254
9.3	Gibberellin signalling and seed germination	264
9.3.1	The <i>GID1ac</i> and <i>GID1b</i> pathways in seeds	264
9.3.2	DELLA proteins and seed germination	268
9.4	Gibberellin and abiotic stress factors: thermoinhibition of seed germination	270
9.5	Gibberellin and biotic stress factors: allelochemical interference of gibberellin biosynthesis during seed germination	273

9.6	Conclusions and perspectives	276
	Acknowledgements	277
	References	277
10	Gibberellins and Plant Vegetative Growth	285
	<i>Cristina Martínez, Ana Espinosa-Ruiz and Salomé Prat</i>	
10.1	Introduction	285
10.2	Gibberellins and shoot development	288
10.2.1	Control of SAM function and leaf size	289
10.2.2	Elongation of the hypocotyl	290
10.2.3	Apical hook formation	295
10.3	Gibberellin function in root development	298
10.3.1	Hormonal control of root growth	298
10.3.2	Gibberellin signalling from the endodermis	302
10.3.3	DELLAs downstream signalling in the root	304
10.3.4	DELLAs promote mycorrhizal symbiosis	306
10.4	Growth under unfavourable conditions	308
10.4.1	DELLAs promote resistance to abiotic stress	308
10.4.2	DELLAs and biotic stress	310
10.5	Concluding remarks	311
	References	312
11	Gibberellins and Plant Reproduction	323
	<i>Andrew R.G. Plackett and Zoe A. Wilson</i>	
11.1	Introduction	323
11.2	The floral transition	324
11.2.1	Gibberellin promotes flowering through multiple interacting pathways	324
11.2.2	Sites of gibberellin biosynthesis and action during the floral transition	329
11.2.3	Gibberellin and flowering in perennial species	331
11.3	Floral development	331
11.3.1	Floral patterning and early development	332
11.3.2	Gibberellin and fertility	334
11.4	Seed and fruit development	340
11.4.1	Fruit development	341
11.4.2	Embryo and seed development	345
	Acknowledgements	348
	References	348
12	Chemical Regulators of Gibberellin Status and their Application in Plant Production	359
	<i>Wilhelm Rademacher</i>	
12.1	Introduction	359
12.2	Gibberellins	361

12.3	Inhibitors of gibberellin biosynthesis	363
12.3.1	Quaternary ammonium compounds	365
12.3.2	Compounds with a nitrogen-containing heterocycle	366
12.3.3	Structural mimics of 2-oxoglutaric acid	369
12.3.4	16,17-Dihydro-gibberellins	371
12.4	Uses for gibberellins and inhibitors of gibberellin biosynthesis in crop production	372
12.4.1	Wheat, barley, rye, oats and other small-grain cereals	373
12.4.2	Rice	376
12.4.3	Sugarcane	377
12.4.4	Pasture and turf grasses	377
12.4.5	Oilseed rape	379
12.4.6	Cotton	379
12.4.7	Peanuts	381
12.4.8	Opium poppy	382
12.4.9	Fruit trees growing in temperate climate	382
12.4.10	Fruit and nut trees growing in subtropical and tropical climates	385
12.4.11	Grapevines	387
12.4.12	Ornamentals	389
12.4.13	Hybrid seed production	391
12.5	Outlook	391
	References	391
13	Genetic Control of Gibberellin Metabolism and Signalling in Crop Improvement	405
	<i>Andrew L. Phillips</i>	
13.1	Introduction	405
13.2	The <i>REDUCED HEIGHT-1 (Rht-1)</i> alleles of wheat	406
13.2.1	Pleiotropic effects of <i>Rht-1</i> alleles	410
13.2.2	<i>Rht-1</i> orthologues in other crop species	412
13.3	The <i>SEMI-DWARF-1 (SD-1)</i> alleles of rice	413
13.4	The <i>ELONGATED UPPERMOST INTERNODE (EUI)</i> gene of rice	415
13.5	Commercially useful alleles of other genes from the gibberellin pathway	416
13.6	Transgenic approaches to manipulation of gibberellin-dependent processes in crops	419
13.6.1	Cereals	419
13.6.2	Other crop species	420
13.7	Conclusions	423
	Acknowledgements	424
	References	424
Appendix	The structures of the gibberellins	431
Index		437