

Contents

Contributors	xv
Preface	xvii
1 Mitotic senescence in plants	1
SUSHENG GAN	
1.1 Introduction	1
1.2 Terminology and types of senescence	1
1.3 Plants exhibit mitotic senescence, postmitotic senescence and cell quiescence	3
1.4 Mitotic senescence: arrest of SAM	4
1.4.1 Initiation of SAM	4
1.4.2 Maintenance of SAM	4
1.4.3 Arrest of SAM: a mitotic senescence in nature	5
1.4.3.1 Physiological regulation	5
1.4.3.2 Genetic regulation	7
1.5 Role of telomere and telomerase in mitotic senescence	7
1.5.1 Telomere	7
1.5.2 Telomerase	7
1.5.3 Telomere shortening and replicative senescence in animals	8
1.5.4 Telomere biology in plants	8
1.6 Closing remarks	9
Acknowledgment	10
References	10
2 Chlorophyll catabolism and leaf coloration	12
STEFAN HÖRTENSTEINER AND DAVID W. LEE	
2.1 Introduction	12
2.2 Chlorophyll catabolites	12
2.2.1 Green catabolites	12
2.2.1.1 Chlorins	12
2.2.1.2 Phytol	15
2.2.2 Catabolites with a tetrapyrrolic structure	15
2.2.2.1 Red chlorophyll catabolites	15
2.2.2.2 Fluorescent chlorophyll catabolites	16

2.2.2.3	Nonfluorescent chlorophyll catabolites	16
2.2.2.4	Are NCCs degraded further?	17
2.3	The chlorophyll degradation pathway	18
2.3.1	Chlorophyll cycle	18
2.3.2	Reactions on green pigments	18
2.3.2.1	Chlorophyllase	18
2.3.2.2	Mg dechelation	19
2.3.3	Loss of green color	20
2.3.3.1	Pheophorbide a oxygenase	20
2.3.3.2	Red chlorophyll catabolite reductase	21
2.3.4	Reactions on pFCC	21
2.3.4.1	Hydroxylation	21
2.3.4.2	Glucosylation	22
2.3.4.3	Malonylation	22
2.3.4.4	Demethylation	22
2.3.4.5	Tautomerization	22
2.4	Chlorophyll catabolic mutants	23
2.5	Significance of chlorophyll breakdown	23
2.5.1	Topology of chlorophyll breakdown	23
2.5.2	Chl breakdown and cell death	24
2.5.3	Chl breakdown and nitrogen economy	25
2.6	The pigments of senescing leaves	26
2.7	The function of anthocyanins in leaf senescence	28
2.7.1	Physiological explanations	28
2.7.2	Ecological explanations	29
2.7.3	Reconciling these explanations	30
2.8	Conclusions and perspectives	30
	References	31
3	Membrane dynamics and regulation of subcellular changes during senescence	39
	MARIANNE HOPKINS, LINDA McNAMARA, CATHERINE TAYLOR, TZANN-WEI WANG AND JOHN THOMPSON	
3.1	Introduction	39
3.2	Loss of membrane structural integrity during senescence	40
3.2.1	Senescence-associated changes in the molecular organization of membrane lipid bilayers	40
3.2.2	Role of lipases	42
3.2.2.1	Initial fate of de-esterified fatty acids in senescing membranes	43
3.2.2.2	Autocatalytic nature of membrane fatty acid de-esterification	44
3.2.3	Role of galactolipases	45
3.3	Role of proteolysis in membrane senescence	48

3.4	Dismantling of membranes in senescing tissue	51
3.4.1	Plastoglobuli	51
3.4.2	Cytosolic lipid-protein particles	54
3.4.2.1	Sites of cytosolic lipid-protein particle ontogeny	54
3.5	Role of autophagy	55
3.6	Metabolism of membrane fatty acids in senescing tissues	57
3.6.1	Galactolipid fatty acids	58
3.6.2	Fate of thylakoid fatty acids during stress-induced senescence	59
3.7	Translational regulation of senescence	61
	References	62
4	Oxidative stress and leaf senescence	69
	ULRIKE ZENTGRAF	
4.1	Introduction	69
4.2	Antioxidative capacity, oxidative stress and life span	71
4.3	Antioxidants	72
4.4	ROS signaling	74
4.5	Role of different cell compartments	77
4.5.1	Peroxisomes	77
4.5.2	Chloroplasts	78
4.5.3	Mitochondria	79
4.5.4	Nucleus	80
4.6	Concluding remarks	81
	References	81
5	Nutrient remobilization during leaf senescence	87
	ANDREAS M. FISCHER	
5.1	Overview	87
5.2	Macro- and micronutrient remobilization	88
5.2.1	Carbon	89
5.2.2	Sulfur	90
5.2.3	Phosphorus	90
5.2.4	Potassium	91
5.2.5	Magnesium, calcium and micronutrients	91
5.3	Nitrogen remobilization	92
5.3.1	Protein degradation in senescing leaves	93
5.3.1.1	Classification of peptidases	93
5.3.1.2	Compartmentation of peptidases	94
5.3.1.3	Regulation of peptidases during leaf senescence	96
5.3.2	Amino acid metabolism in senescing leaves	98
5.3.3	Nitrogen transport to developing sinks	99

5.4	Outlook	101
	Acknowledgments	102
	References	102
6	Environmental regulation of leaf senescence	108
	AMNON LERS	
6.1	Introduction	108
6.2	Light irradiance	111
6.2.1	Light intensity	111
6.2.1.1	Low light	111
6.2.1.2	Darkness	112
6.2.1.3	High light	113
6.2.2	Photoperiod	114
6.2.3	Wavelength	114
6.2.3.1	Red/Far red	114
6.2.3.2	Blue light	116
6.2.3.3	Ultraviolet	116
6.3	Ozone	118
6.4	Temperature	119
6.5	Drought stress	120
6.6	Flooding	121
6.7	Salinity	122
6.8	Environmental pollution – toxic materials	123
6.9	Oxidative stress involvement in environmental regulation of senescence	124
6.10	Nutrient/mineral shortage	125
6.11	Atmospheric CO ₂	126
6.12	Biotic stress	127
6.13	Concluding remarks	130
	References	133
7	Developmental and hormonal control of leaf senescence	145
	JOS H.M. SCHIPPERS, HAI-CHUN JING, JACQUES HILLE AND PAUL P. DIJKWEL	
7.1	Introduction	145
7.2	Developmental senescence: a plant genome is optimised for early survival and reproduction	145
7.3	Developmental processes that regulate leaf senescence	147
7.3.1	Reactive oxygen species	147
7.3.2	Metabolic flux	148
7.3.3	Protein degradation	148
7.4	Hormonal control of leaf senescence	149
7.4.1	Hormones that delay leaf senescence	150
7.4.1.1	Gibberellic acid	150
7.4.1.2	Auxin	150
7.4.1.3	Cytokinins	151

7.4.2	Hormones that induce leaf senescence	152
7.4.2.1	ABA	152
7.4.2.2	Brassinosteroids	153
7.4.2.3	Ethylene	154
7.4.2.4	Jasmonic acid	156
7.4.2.5	Salicylic acid	157
7.5	Involvement of genome programmes in the regulation of senescence-associated genes	157
7.6	Integrating hormonal action into developmental senescence	161
7.7	Outlook and perspectives	163
	References	164
8	The genetic control of senescence revealed by mapping quantitative trait loci	171
	HELEN OUGHAM, IAN ARMSTEAD, CATHERINE HOWARTH, ISAAC GALYUON, IAIN DONNISON AND HOWARD THOMAS	
8.1	Quantitative traits – what they are and how they are mapped	171
8.1.1	Genetic mapping	171
8.1.2	Major genes and QTL	171
8.1.3	QTL mapping	171
8.1.4	'QTL for' talk	173
8.2	Biomarkers of the senescence process	174
8.2.1	Senescence is polygenic and quantitative	174
8.2.2	Trait measurement in senescence	174
8.2.3	Pseudosenescence	174
8.2.4	Senescence-specific metabolism	175
8.3	Correlated developmental events as second-order senescence traits	175
8.3.1	Remote control of senescence	175
8.3.2	Allometry and QTL	175
8.3.3	QTL mapping as a tool for holistic analysis of development	177
8.4	G × E and the contribution of biotic and abiotic factors	177
8.4.1	Elasticity and plasticity	177
8.4.2	G × E and the now-you-see-it, now-you-don't QTL	177
8.4.3	Implications for the design and conduct of QTL experiments	177
8.5	Case studies	178
8.5.1	Rice	178
8.5.2	Sorghum and millet	181
8.5.3	Maize	184
8.5.4	Wheat and barley	186
8.5.5	Other species	188

8.6	Exploitation of QTL mapping for senescence traits	189
8.6.1	Model species, comparative mapping and the role of bioinformatics	189
8.6.2	Introgression landing	192
8.6.3	Integration with omics and other technologies	193
8.6.4	QTL as breeding tools	194
8.7	QTL, senescence, ageing and death	195
	Acknowledgments	195
	References	195
9	Genomics and proteomics of leaf senescence	202
	MARIE-JEANNE CARP AND SHIMON GEPSTEIN	
9.1	Introduction	202
9.2	Transcriptomics of leaf senescence	203
9.2.1	Technologies	203
9.2.1.1	Differential display, <i>in situ</i> hybridization and subtractive hybridization	203
9.2.1.2	Microarrays	204
9.2.2	Altering the expression of senescence-specific genes may extend the lifespan of annual plants	205
9.2.3	From single to global gene expression studies of leaf senescence	206
9.2.4	Kinetics studies of gene expression define sequential changes in the pathway of the senescence program	207
9.2.5	Classification of the SAGs into functional classes suggests potential regulatory and biochemical pathways occurring during senescence	209
9.2.6	Stress-induced and developmental senescence can be compared by genomic studies	211
9.2.7	Signaling pathways of the senescence program can be elucidated by global gene expression studies	213
9.2.8	Global gene expression studies reveal that autumn leaf senescence has much in common with the senescence in annual plants	215
9.3	Proteomics of leaf senescence	216
9.3.1	Technologies	216
9.3.1.1	Two-dimensional gel electrophoresis	216
9.3.1.2	Liquid chromatography	217
9.3.1.3	Mass spectrometry	217
9.3.1.4	ESI mass spectrometry	219
9.3.2	Current information on leaf senescence proteomic is limited	219
9.3.3	Functional categories of senescence-enhanced proteins	223

9.3.4	Senescence upregulated proteins involved in respiration and various associated metabolic processes	223
9.3.5	Degradation and transport processes	224
9.3.6	Upregulated proteins related to stress and defense mechanisms	225
9.3.7	Comparison between pattern of changes in mRNA and protein levels during senescence indicates partial correlation	225
9.4	Conclusions	227
	References	227
10	Molecular regulation of leaf senescence	231
	HYO JUNG KIM, PYUNG OK LIM AND HONG GIL NAM	
10.1	Introduction	231
10.1.1	Leaf senescence	231
10.1.2	Senescence-associated genes	231
10.2	Isolation and classification of SAGs	232
10.2.1	Isolation of SAGs	232
10.2.2	Functional classification of SAGs	233
10.2.2.1	Macromolecule degradation	233
10.2.2.2	Nutrient salvage and translocation	234
10.2.2.3	Defence and detoxification genes	234
10.2.2.4	Regulatory genes	234
10.2.3	Comparison of SAGs in various plant species	236
10.3	Regulatory modes of SAGs	237
10.3.1	Temporal regulation of SAGs during senescence	238
10.3.2	Regulation of SAGs by various endogenous and external factors	239
10.3.3	Cis-acting regulatory elements of SAGs	240
10.4	Molecular regulatory mechanisms of leaf senescence	241
10.4.1	Developmental ageing	242
10.4.2	Internal factors	245
10.4.2.1	Phytohormones	245
10.4.2.2	Sugar signalling	247
10.4.3	External factors	248
10.4.4	Regulatory role of protein degradation	248
10.5	Conclusions and future challenges	249
	Acknowledgment	250
	References	250
11	Flower senescence	256
	MICHAEL S. REID AND JEN-CHIH CHEN	
11.1	Introduction	256
11.2	Flower opening and senescence	256

11.3	Model systems	257
11.4	Hormonal regulation of flower senescence	258
11.4.1	Ethylene	258
11.4.2	Abscissic acid	259
11.4.3	Cytokinins	260
11.4.4	Gibberellic acid	260
11.4.5	Auxin	261
11.4.6	Jasmonic acid	261
11.4.7	Polyamines	261
11.4.8	Sugars	262
11.5	Flower senescence and remobilization of resources	263
11.5.1	Protein degradation	263
11.5.2	Nucleic acid degradation	264
11.5.3	Membrane degradation	264
11.5.4	Cell wall changes	265
11.6	Petal senescence as programmed cell death	265
11.7	Molecular biology of petal senescence	267
11.7.1	Senescence-associated genes	267
11.7.2	Functional analysis of SAGs	268
11.7.2.1	Ethylene-dependent senescence	269
11.7.2.2	Ethylene-independent senescence	269
11.7.3	Regulation of petal senescence – a regulatory network?	270
11.7.4	New frontier: prohibitins – mitochondrial proteins with a possible role in floral senescence	272
	References	272
12	Fruit ripening and its manipulation	278
	JAMES J. GIOVANNONI	
12.1	Introduction	278
12.2	Physiologies of ripening fruit	279
12.2.1	Climacteric ripening	279
12.2.2	Nonclimacteric ripening	279
12.3	Model ripening systems	280
12.3.1	Tomato – the model for climacteric ripening	280
12.3.1.1	Tomato genomic resources facilitate ripening research	282
12.3.2	Additional model systems for ripening research	282
12.4	Ripening processes and their manipulation	285
12.4.1	Cell-wall metabolism	285
12.4.2	Ethylene biosynthesis and perception	288
12.4.3	Global ripening control	291
12.4.4	Modification of specific ripening pathways: pigmentation	292

12.5 Summary	294
References	295
13 Genetic manipulation of leaf senescence	304
YONGFENG GUO AND SUSHENG GAN	
13.1 Introduction	304
13.2 Strategies of manipulating leaf senescence	304
13.3 IPT-based transgenic techniques for manipulation of cytokinin production	305
13.4 Development of the SAG12- <i>IPT</i> autoregulatory cytokinin production system	306
13.5 Use of the SAG12- <i>IPT</i> to manipulate senescence in crops	307
13.5.1 <i>IPT</i> expression and cytokinin production in transgenic plants	312
13.5.2 Delayed leaf senescence in the SAG- <i>IPT</i> plants	313
13.5.3 Delayed floral senescence in the SAG12- <i>IPT</i> plants	314
13.5.4 Delayed postharvest senescence in the SAG12- <i>IPT</i> plants	314
13.5.5 Increased yield and biomass production in the SAG12- <i>IPT</i> plants	315
13.5.6 Increased stress tolerance in the SAG12- <i>IPT</i> plants	315
13.6 Other strategies for manipulation of leaf senescence	316
13.7 Closing remarks	317
Acknowledgment	317
References	317
Index	323