

Contents

Contributors	xi
Preface	xiii
1 Cell separation and adhesion processes in plants	1
JEREMY ROBERTS AND ZINNIA GONZALEZ-CARRANZA	
1.1 Introduction	1
1.2 Cell separation processes	2
1.3 Cell adhesion processes	3
1.4 Manipulation of cell separation and adhesion in crop plants	4
1.5 Conclusions	5
References	5
2 Cell wall structure, biosynthesis and assembly	8
AARON H. LIEPMAN, DAVID M. CAVALIER, OLIVIER LEROUXEL AND KENNETH KEEGSTRA	
2.1 Introduction	8
2.2 Primary cell walls: composition and biosynthesis	9
2.2.1 Cellulose	9
2.2.2 Callose	12
2.2.3 Hemicelluloses	12
2.2.3.1 Xyloglucan	14
2.2.3.2 Arabinoxylan	16
2.2.3.3 Galacto(gluco)mannan	16
2.2.3.4 Mixed-linkage glucan	17
2.2.4 Pectic polymers	17
2.2.4.1 Homogalacturonans	19
2.2.4.2 Rhamnogalacturonan I	20
2.2.4.3 Rhamnogalacturonan II	20
2.2.5 Cell wall structural proteins	22
2.3 Cell wall architecture	23
2.4 Primary cell wall expansion and regulation	23
2.4.1 Cellulose deposition and orientation	23
2.4.2 Hemicelluloses and their reorganization	25
2.4.2.1 Expansins	25
2.4.2.2 Xyloglucan endotransglucosylase/hydrolases	26
2.4.3 Pectins involved in cell wall structure and intercellular adhesion	27

2.5	Concluding remarks	28
	Acknowledgements	28
	References	28
3	Vascular cell differentiation	40
	HIDEO KURIYAMA AND HIROO FUKUDA	
3.1	TE differentiation as a model of cell-cell connection	40
3.2	Early processes induced by cell separation	41
3.3	Factors that regulate TE cell differentiation	43
3.3.1	Auxin	43
3.3.2	Plant sterols	44
3.3.3	Xylogen	45
3.4	Effects of tissue organization on cell differentiation	45
3.5	Cell wall components characteristic of TE and/or vascular cells	46
3.5.1	Cellulose	46
3.5.2	Hemicellulose	47
3.5.3	Pectin	48
3.5.4	Lignin	49
3.5.5	Cell wall component proteins	50
3.6	The degradation of TE primary cell walls and pore formation	51
3.7	Co-regulation of cell wall degradation and PCD	55
3.8	Conclusion	58
	References	59
4	Cell adhesion, separation and guidance in compatible plant reproduction	69
	JEAN-CLAUDE MOLLET, CÉLINE FAUGERON AND HENRI MORVAN	
4.1	Introduction	69
4.2	Pollen formation and microspore separation	71
4.2.1	Pollen mother cell and tetrad walls	71
4.2.2	Microspore separation	72
4.2.3	Pollen grain wall and pollen coat	73
4.3	Pollen-stigma adhesion and pollen tube guidance	73
4.3.1	Adhesion of pollen grain	73
4.3.2	Pollen tube emergence and guidance on the stigma	76
4.4	Adhesion and guidance of pollen tubes in the style	77
4.4.1	Proline/hydroxyproline-rich glycoproteins	77
4.4.1.1	Pollen and pistil AGPs	77
4.4.1.2	Pex, pollen-specific leucine-rich repeat extensin chimeras	78
4.4.2	Pollen and pistil cysteine-rich proteins	79
4.4.2.1	SCA-pectin complex	79

4.4.2.2	Cys-rich protein's interaction with pollen LRR receptor kinases	79
4.4.3	Wall-associated kinases	81
4.5	Cell wall modifying proteins and pollen tube growth in the ECM	81
4.5.1	Cell wall modifying proteins from pollen	81
4.5.2	Cell-wall-modifying proteins in the pistil	82
4.6	Pollen tube adhesion, interaction and guidance in the ovary	82
4.6.1	Pollen tube attraction by sporophytic cells	83
4.6.2	Pollen tube guidance by gametophytic cells	83
4.6.3	Interaction during fertilization: female control of male gamete delivery	84
4.7	Conclusions and perspectives	84
	Acknowledgements	85
	References	85
5	Cell separation in roots	91
	FUSHI WEN, MARTA LASKOWSKI AND MARTHA HAWES	
5.1	Introduction: cell wall solubilization by microbial enzymes: a framework for understanding cell wall solubilization by plant enzymes	91
5.2	Cell wall solubilization in plants: border cell separation in legumes as a model	93
5.2.1	Border cell separation	94
5.2.2	Pectolytic enzyme activity present in the root cap, and correlated with border cell separation	95
5.2.3	Pectinmethylesterase and border cell separation	95
5.3	Other mechanisms of cap turnover	98
5.4	Cortical cell sloughing and lateral root emergence	100
5.4.1	Evidence for the involvement of PME	100
5.4.2	Evidence for the involvement of polygalacturonase	101
5.4.3	Evidence for involvement of pectate lyase	101
5.5	Aerenchyma	102
	References	102
6	Organ abscission	106
	MICHELLE E. LESLIE, MICHAEL W. LEWIS AND SARAH J. LILJEGREN	
6.1	Introduction	106
6.2	Setting the stage: patterning and differentiation	111
6.2.1	BLADE ON PETIOLE1 and 2 establish lateral organ polarity	111
6.2.2	SEEDSTICK promotes proper development of the seed stalk	113

6.2.3	JOINTLESS is essential for differentiation of the pedicel abscission zone	114
6.2.4	Jointless-2 maps near a predicted transcriptional regulator	115
6.3	Communication involved in cell separation	115
6.3.1	Involvement of the ethylene-signaling pathway	116
6.3.1.1	ETHYLENE RECEPTOR1 links ethylene perception with abscission initiation	117
6.3.1.2	The NEVER-RIPE ethylene receptor promotes abscission in tomato	117
6.3.1.3	Never-ripe2 and green-ripe may represent mutations in a novel ethylene signaling gene	118
6.3.1.4	ETHYLENE-INSENSITIVE2, a transmembrane protein of unknown function, is required for the proper timing of abscission	118
6.3.1.5	EIN3-LIKE1, 2 and 3 may induce the transcription of abscission-related genes	119
6.3.2	Ethylene-independent avenues to abscission	119
6.3.2.1	INFLORESCENCE DEFICIENT IN ABSCISSION encodes a putative signaling ligand essential for abscission	119
6.3.2.2	HAESA, a receptor-like kinase, may perceive an abscission signal	120
6.3.2.3	DELAYED ABSCISSION mutations uncouple the initiation of abscission from ethylene signaling	121
6.3.2.4	ACTIN-RELATED PROTEINS may globally regulate transcription during senescence and abscission	121
6.3.2.5	Transcriptional activity of AGAMOUS-LIKE 15 inhibits senescence and abscission	122
6.3.3	Integrative pathways that promote ethylene biosynthesis and abscission	123
6.3.3.1	AUXIN RESPONSE FACTORS regulate the timing of abscission	123
6.3.3.2	G-protein signaling promotes ethylene biosynthesis and abscission of citrus leaves	124
6.4	Dissolution of the cell wall – cell separation	125
6.4.1	Hydrolytic enzymes	125
6.4.1.1	Endo- β -1,4-glucanases	125
6.4.1.2	Polygalacturonases	126
6.4.2	Expansins	128
6.4.2.1	Expansins positioned to affect cell wall loosening during abscission	128
6.5	Discussion and future directions	129
	Acknowledgments	130
	References	130

7 Dehiscence	137
LARS ØSTERGAARD, BERNHARD BORKHARDT AND PETER ULVSKOV	
7.1 Introduction	137
7.2 Shatter resistance	138
7.3 Morphogenesis and anatomy of the dehiscence zone	140
7.3.1 Brassicaceae fruit morphology	141
7.3.2 Fabaceae fruit morphology	142
7.4 Cell wall dissolution and its hormonal regulation	143
7.5 Factors regulating Arabidopsis fruit development	150
7.5.1 The FRUITFULL gene	150
7.5.2 The SHATTERPROOF genes	151
7.5.3 The INDEHISCENT gene	151
7.5.4 The ALCATRAZ gene	151
7.5.5 The REPLUMLESS gene	152
7.6 Genetic interactions during Arabidopsis fruit development	152
7.7 Anther dehiscence	155
7.8 Prospects for engineering shatter resistance	156
7.9 Development of model-to-crop approaches	158
Acknowledgments	158
References	159
 8 Fruit ripening	 164
CATHERINE MARTEL AND JAMES GIOVANNONI	
8.1 Introduction	164
8.2 Fruits	164
8.2.1 Fruit physiology	164
8.2.2 Fruit development	164
8.2.3 Fleshy fruit ripening	165
8.2.4 Tomato as a fleshy fruit model for ripening	166
8.3 Regulation of ripening	166
8.3.1 Ethylene-regulated ripening	166
8.3.2 Biosynthesis	167
8.3.3 Signalling	167
8.3.4 Developmentally regulated ripening	168
8.3.5 Developmental mutants	168
8.4 Cell wall metabolism during fruit ripening	170
8.4.1 Fruit cell wall composition	170
8.4.2 Ripening-induced cell wall modifications	170
8.5 Cell wall modifying enzymes	171
8.5.1 Pectin and pectinases	171
8.5.1.1 Polygalacturonase	172
8.5.1.2 Pectin methyl esterases	172
8.5.1.3 Pectate lyase	173
8.5.1.4 β -galactosidase/arabinosidases	173

8.5.2	Cellulose and cellulose-modifying enzymes	174
8.5.2.1	Endo-1,4- β -glucanases	174
8.5.3	Expansins	174
8.5.4	Hemicellulose and hemicellulases	175
8.6	Colourless non-ripening mutant: a model to study fruit ripening cell wall modifications	175
8.7	Conclusions	176
	References	176
9	The role of polymer cross-linking in intercellular adhesion	183
	KEITH W. WALDRON AND CHRISTOPHER T. BRETT	
9.1	Introduction	183
9.2	The location of intercellular cross-links within the wall	185
9.2.1	Cell adhesion at tricellular junctions	186
9.2.1.1	Intercellular space formation	186
9.2.1.2	Studies of the cell surface after cell separation	187
9.2.1.3	Chemical nature of components at the edge of the cell face	188
9.2.1.4	Mathematical modelling	188
9.2.2	Cell adhesion in locations other than the tricellular junction	189
9.2.3	Role of secondary thickening in cell adhesion	189
9.3	The nature of intercellular polymers and their cross-links	190
9.3.1	Role of pectic polysaccharides and their cross-links in intercellular adhesion	190
9.3.1.1	Evidence for the involvement of pectic polymers in cell adhesion	190
9.3.1.2	Nature of pectic polymers and their cross-links	191
9.3.2	Cell adhesion and pectin biosynthesis	193
9.3.2.1	Pectin biosynthesis	193
9.3.2.2	Pectin modification in muro	194
9.3.2.3	Possible mechanisms for the generation of specific patterns of pectin methylation at the edges of cell faces	194
9.3.2.4	Other possible linkages	195
9.3.3	Phenolics in the primary wall and middle lamella	195
9.3.3.1	Studies on Chinese water chestnut	196
9.3.3.2	Asparagus	196
9.3.3.3	Sugar beet	198
9.3.4	Cell adhesion and the biosynthesis of feruloylated wall polymers	199
9.3.5	The Hard-To-Cook defect	199
9.4	Conclusions	200
	Acknowledgements	200
	References	200
	Index	205