

Contents

Part I Evolution and Population Genetics of Self-Incompatibility

| | | |
|----------|--|----|
| 1 | New Insights on Heterostyly: Comparative Biology, Ecology and Genetics | 3 |
| | S.C.H. Barrett and J.S. Shore | |
| 1.1 | Introduction | 4 |
| 1.2 | Comparative Biology and Evolutionary History of Heterostyly ... | 6 |
| 1.2.1 | Phylogeny Reconstruction and Character Evolution | 7 |
| 1.3 | Function and Reproductive Ecology of Heterostyly | 10 |
| 1.3.1 | Function of Heterostyly | 10 |
| 1.3.2 | Floral Morph Ratios and Reproductive Success | 12 |
| 1.4 | Inheritance of Heterostyly and the Supergene Model | 14 |
| 1.4.1 | Inheritance of Distyly and Tristyly | 14 |
| 1.4.2 | Supergene Model | 15 |
| 1.4.3 | Mutational Analyses and the Study of Genetic Variants .. | 19 |
| 1.5 | Molecular Genetics | 19 |
| 1.5.1 | Theoretical Models and Predictions | 20 |
| 1.5.2 | Protein Profiles | 22 |
| 1.5.3 | mRNA Expression | 22 |
| 1.5.4 | Genetic Localization | 23 |
| 1.6 | Concluding Remarks | 25 |
| | References | 26 |
| 2 | Genetic and Environmental Causes and Evolutionary Consequences of Variations in Self-Fertility in Self Incompatible Species | 33 |
| | S.V. Good-Avila, J.I. Mena-Alí, and A.G. Stephenson | |
| 2.1 | Introduction | 34 |
| 2.2 | Genetics of Self-Fertility | 35 |
| 2.2.1 | Mutations Affecting the <i>S</i> -locus | 36 |
| 2.2.2 | Unlinked Modifiers of SI | 37 |

| | | |
|----------|---|-----------|
| 2.2.3 | Plasticity in Self-Fertility | 40 |
| 2.2.4 | Summary of Genetics of Self-Fertility | 41 |
| 2.3 | Fate of Self-Fertility Genes | 42 |
| 2.3.1 | Conditions for Stable Polymorphisms | 43 |
| 2.3.2 | Summary and Conclusions Concerning Stable Polymorphisms | 45 |
| | References | 47 |
| 3 | On the Evolutionary Modification of Self-Incompatibility: Implications of Partial Clonality for Allelic Diversity and Genealogical Structure | 53 |
| | M. Vallejo-Marín and M.K. Uyenoyama | |
| 3.1 | Introduction | 54 |
| 3.2 | Mating System Dynamics | 55 |
| 3.2.1 | Relative Transition Rates | 55 |
| 3.2.2 | Multiple Origins of SC in <i>Arabidopsis</i> | 55 |
| 3.2.3 | Modified Forms of SI | 56 |
| 3.3 | S-Locus Evolution Under Partial Clonality | 57 |
| 3.3.1 | Diffusion Approximation | 57 |
| 3.3.2 | S-Allele Number and Frequency | 60 |
| 3.3.3 | Age of the Root | 62 |
| 3.4 | Discussion | 65 |
| 3.4.1 | Clonality in the Solanaceae | 65 |
| 3.4.2 | Evolutionary Stability of Partial SI | 65 |
| 3.4.3 | Paradoxical Effects on Mating Systems | 66 |
| 3.5 | Conclusions | 67 |
| | Appendix 1: Diffusion Equation Approximation | 68 |
| | Appendix 2: Simulations | 69 |
| | References | 69 |
| 4 | Evolution and Phylogeny of Self-Incompatibility Systems in Angiosperms | 73 |
| | A.M. Allen and S.J. Hiscock | |
| 4.1 | Introduction | 74 |
| 4.1.1 | Diversity of SI Systems in Angiosperms | 75 |
| 4.1.2 | Evolutionary Origin(s) of SI Systems | 76 |
| 4.2 | Was Self-Incompatibility Present in the First Angiosperms? | 77 |
| 4.2.1 | Self-Incompatibility in Basal Angiosperms | 78 |
| 4.2.2 | Self-Incompatibility in the Monocots | 80 |
| 4.3 | Phylogenetic Distribution of SI Systems | 81 |
| 4.3.1 | Late-Acting Ovarian Self Incompatibility (OSI) | 84 |
| 4.3.2 | Gametophytic Self-Incompatibility (GSI) | 86 |
| 4.3.3 | Sporophytic Self-Incompatibility (SSI) | 88 |
| 4.4 | The Relationship Between GSI and SSI | 89 |
| 4.5 | Discussion | 91 |
| | References | 95 |

| | | |
|---|---|-----|
| 5 | What Genealogies of S-alleles Tell Us | 103 |
| | J.R. Kohn | |
| 5.1 | Introduction | 104 |
| 5.2 | Long-Term Demographic Information from the <i>S</i> -locus | 105 |
| 5.3 | Implications of Shared Ancestral Polymorphism | 108 |
| 5.3.1 | Tracing the History of Mating System Change | 108 |
| 5.3.2 | Diversification Rate Differences and Character State Reconstruction | 110 |
| 5.4 | The Pace of New Allele Formation | 111 |
| 5.5 | Remaining Issues of S-RNase Evolution | 112 |
| 5.6 | Pollen Specificity Genes | 114 |
| 5.7 | Conclusions | 117 |
| | References | 117 |
| 6 | Self-Incompatibility and Evolution of Mating Systems in the Brassicaceae | 123 |
| | S. Sherman-Broyles and J.B. Nasrallah | |
| 6.1 | Introduction | 124 |
| 6.2 | Structural and Sequence Diversification of <i>S</i> -locus Haplotypes and Their Recognition Genes | 125 |
| 6.2.1 | Conserved and Diverged Features of the <i>S</i> -locus | 127 |
| 6.2.2 | Intra-Specific Structural Heteromorphism and Sequence Polymorphism: Suppressed Recombination and Maintenance of SRK-SCR Linkage | 128 |
| 6.2.3 | Diversification of the <i>S</i> -locus Genes and the SI Recognition Repertoire | 130 |
| 6.3 | Evolutionary Switches from Self-Incompatibility to Self-Fertility | 135 |
| 6.3.1 | Molecular Genetics of Switches to Self-Fertility | 136 |
| 6.3.2 | Breakdown of SI by Disruption of <i>S</i> -locus Gene Expression in Inter-Specific Hybrids | 137 |
| 6.3.3 | The Case of Self-Fertility in <i>A. thaliana</i> | 138 |
| 6.4 | Future Prospects | 142 |
| | References | 142 |
| Part II Molecular and Cell Biology of Self-Incompatibility Systems | | |
| 7 | Milestones Identifying Self-Incompatibility Genes in Brassica Species: From Old Stories to New Findings | 151 |
| | M. Watanabe, G. Suzuki, and S. Takayama | |
| 7.1 | Self-Incompatibility as an Agriculturally Important Trait | 152 |
| 7.2 | The First Milestone: Bateman's Idea for Sporophytic Control of the <i>S</i> -locus | 154 |
| 7.3 | The Second Milestone: Identification of SLG by Using IEF | 155 |
| 7.4 | The Third Milestone: Identification of <i>SRK</i> , the Female <i>S</i> Determinant Gene | 156 |

| | | |
|----------|---|------------|
| 7.5 | The Fourth Milestone: Functional Evidences of <i>SRK</i> in SI | 157 |
| 7.6 | The Fifth Milestone: Establishment of Bioassay System | 158 |
| 7.7 | The Sixth Milestone: Identification of <i>SP11/SCR</i> , the Male <i>S</i> Determinant Gene | 159 |
| 7.8 | After Identifying the SI Genes and Future Milestones | 160 |
| 7.8.1 | Demonstrating Physical Interaction Between SRK and SP11/SCR | 160 |
| 7.8.2 | Downstream of the Interaction: Identifying Components and Mechanisms Involved in Mediating the Rejection of Self Pollen | 162 |
| 7.8.3 | Molecular Mechanisms of Dominance Relationships | 163 |
| 7.8.4 | Evolution of SI Genes | 164 |
| 7.9 | Prospects | 165 |
| | References | 166 |
| 8 | ‘Self’ Pollen Rejection Through the Intersection of Two Cellular Pathways in the Brassicaceae: Self-Incompatibility and the Compatible Pollen Response | 173 |
| | M.A. Samuel, D. Yee, K.E. Haasen, and D.R. Goring | |
| 8.1 | Introduction | 174 |
| 8.2 | The Early Stages of Compatible Pollen–Stigma Interactions in the Brassicaceae | 175 |
| 8.2.1 | Pollen Capture and Adhesion | 175 |
| 8.2.2 | Pollen Hydration | 176 |
| 8.2.3 | Pollen Germination and Pollen Tube Penetration | 178 |
| 8.3 | The SI Response Causes Pollen Arrest at the Stigmatic Surface | 179 |
| 8.3.1 | The S Receptor Kinase Activates a Cellular Signalling Pathway in the Stigmatic Papilla to Trigger Self Pollen Rejection | 179 |
| 8.3.2 | The M Locus Protein Kinase acts Together with the S Receptor Kinase to Promote SI | 180 |
| 8.3.3 | The SRK Kinase Domain can Interact with a Range of Intracellular Proteins | 181 |
| 8.3.4 | Thioredoxin h Inhibits SRK Activity in the Absence of Self Pollen | 182 |
| 8.3.5 | ARC1 Functions Downstream of SRK to Promote SI | 182 |
| 8.3.6 | BnExo70A1 is a Potential Substrate for ARC1 and is Required for Compatible Pollen–Stigma Interactions | 184 |
| 8.3.7 | Endomembrane Changes in the Stigmatic Papillae Following Compatible and Self-Incompatible Pollinations in the Brassicaceae | 185 |
| 8.4 | Conclusions and Prospects | 186 |
| | References | 187 |

| | | |
|-----------|---|-----|
| 9 | Molecular Biology of S-RNase-Based Self-Incompatibility | 193 |
| | Y. Zhang and Y. Xue | |
| 9.1 | Introduction | 194 |
| 9.2 | S-RNase Determines S-Specificity in Pistil | 196 |
| 9.2.1 | Isolation and Identification of S-RNase as the Pistil S . . . | 196 |
| 9.2.2 | S-RNase Sequence Features and the Specificity Determinant | 196 |
| 9.2.3 | The Role of S-RNase: A Cytotoxin Specifically Inhibits Self Pollen | 198 |
| 9.3 | F-Box Proteins Determine S-Specificity in Pollen | 199 |
| 9.3.1 | Clues from Pollen-Part Self Compatible Mutants | 199 |
| 9.3.2 | Isolation of the Pollen SI Determinant, SLF/SFB | 200 |
| 9.3.3 | Sequence Analysis of SLFs and SFBs | 201 |
| 9.3.4 | Identification of SLF as the Pollen S | 201 |
| 9.3.5 | SFBs from Rosaceae Likely Represent Another Class of F-Box Genes | 202 |
| 9.4 | Other Genes That Modulate the SI Response | 203 |
| 9.4.1 | The Pistil Modifier Factors | 203 |
| 9.4.2 | The Pollen Modifier Factors | 204 |
| 9.5 | Molecular Mechanisms for S-RNase-based SI | 205 |
| 9.5.1 | Pollen S, the Positive or Negative Regulator of S-RNase? Clues from Genetic Evidence | 205 |
| 9.5.2 | The Fate of S-RNases: S-RNase Restriction is Likely to Involve Ubiquitination | 206 |
| 9.5.3 | Future Perspectives | 208 |
| | References | 210 |
| 10 | Comparing Models for S-RNase-Based Self-Incompatibility | 217 |
| | B. McClure | |
| 10.1 | The Biology of S-RNase-Based SI | 218 |
| 10.1.1 | Genetic Breakdown | 218 |
| 10.2 | S-RNase and S-locus F-box Proteins | 219 |
| 10.2.1 | S-RNase Structure and Specificity | 219 |
| 10.2.2 | S-locus F-Box Genes | 221 |
| 10.3 | Non-S-Specific Genes | 222 |
| 10.3.1 | HT Genes | 223 |
| 10.3.2 | S-RNase Binding Proteins in the Transmitting Tract Extracellular Matrix | 224 |
| 10.3.3 | Non-S-Specific Factors in Pollen | 226 |
| 10.4 | Comparing Models for S-RNase-Based SI | 227 |
| 10.4.1 | How do Compatible Pollen Tubes Resist S-RNase Cytotoxicity? | 227 |
| 10.4.2 | Is There a Separate Mechanism in the Rosaceae? | 227 |
| 10.4.3 | Inhibiting S-RNase Enzyme Activity | 228 |

| | | |
|-----------|--|------------|
| 10.4.4 | S-RNase Degradation | 228 |
| 10.4.5 | S-RNase Compartmentalisation | 231 |
| | References | 233 |
| 11 | Self-Incompatibility in <i>Papaver Rhoeas</i>: Progress in Understanding Mechanisms Involved in Regulating Self-Incompatibility in <i>Papaver</i> | 237 |
| | V.E. Franklin-Tong | |
| 11.1 | Introduction | 238 |
| 11.1.1 | Genetics and Cell Biology of Self-Incompatibility in <i>Papaver</i> | 238 |
| 11.1.2 | How Studies on Self-Incompatibility in <i>Papaver</i> Started | 239 |
| 11.1.3 | The <i>Papaver in Vitro</i> SI System | 241 |
| 11.2 | <i>S</i> Proteins Determine <i>S</i> -Specificity in the Pistil | 242 |
| 11.2.1 | Identification of Pistil <i>S</i> -locus Components | 242 |
| 11.2.2 | Pistil <i>S</i> -Protein Sequence Information and Residues Required for Function | 243 |
| 11.3 | Identification of the Pollen <i>S</i> -Determinant | 243 |
| 11.4 | Mechanisms Involved in SI in the <i>Papaver</i> System | 244 |
| 11.4.1 | Calcium Signalling Mediates <i>Papaver</i> SI | 244 |
| 11.4.2 | A Role for Soluble Inorganic Pyrophosphatases (sPPases) in <i>Papaver</i> SI | 245 |
| 11.4.3 | Alterations to the Actin Cytoskeleton are Triggered by <i>Papaver</i> SI | 246 |
| 11.4.4 | SI Triggers Programmed Cell Death | 247 |
| 11.5 | An Overall Model for Mechanisms Involved in Regulating SI in <i>Papaver</i> | 251 |
| 11.5.1 | A Contrast to the S-RNase System and <i>Brassica</i> SI Systems | 253 |
| 11.6 | Future Perspectives | 254 |
| | References | 255 |
| 12 | Molecular Genetics of Sporophytic Self-Incompatibility in <i>Ipomoea</i>, a Member of the Convolvulaceae | 259 |
| | Y. Kowyama, T. Tsuchiya, and K. Kakeda | |
| 12.1 | Introduction | 260 |
| 12.2 | Sexual Reproduction in the Genus <i>Ipomoea</i> | 261 |
| 12.3 | Genetics of Self-Incompatibility in <i>Ipomoea</i> | 261 |
| 12.4 | Stigma-Specific Proteins | 263 |
| 12.5 | Physical Size of the <i>S</i> -locus | 264 |
| 12.6 | Genomic Organisation of the <i>S</i> -locus | 266 |
| 12.7 | <i>S</i> -locus Genes in <i>Ipomoea</i> | 268 |
| 12.8 | Diversity of the SI Systems | 270 |
| | References | 271 |

| | |
|---|-----|
| 13 Self-Incompatibility in the Grasses | 275 |
| P. Langridge and U. Baumann | |
| 13.1 Introduction | 276 |
| 13.2 Genetic Control of SI in the Grasses | 277 |
| 13.2.1 Features of the <i>S-Z</i> System | 278 |
| 13.2.2 The Third Locus 'T' | 279 |
| 13.2.3 Mechanism of Action of <i>S</i> - and <i>Z</i> -Gene Products | 280 |
| 13.3 Approaches and Progress in Cloning <i>S</i> and <i>Z</i> | 280 |
| 13.3.1 Reverse Genetics | 281 |
| 13.3.2 Forward Genetics | 281 |
| 13.4 Conclusions | 284 |
| References | 285 |
| | |
| 14 Heteromorphic Self-Incompatibility in <i>Primula</i>: Twenty-First Century Tools Promise to Unravel a Classic Nineteenth Century Model System | 289 |
| A. McCubbin | |
| 14.1 Introduction | 290 |
| 14.2 Floral Characteristics of the Mating Types of <i>Primula</i> | 291 |
| 14.2.1 Style | 292 |
| 14.2.2 Stigma | 292 |
| 14.2.3 Corolla Mouth Size | 292 |
| 14.2.4 Anthers | 293 |
| 14.2.5 Pollen | 293 |
| 14.2.6 Self-Incompatibility Specificity | 293 |
| 14.3 Functions of Heteromorphic Characters | 293 |
| 14.4 Physiological Nature of SI | 295 |
| 14.4.1 Site of Operation | 295 |
| 14.4.2 Candidate Molecules in the Operation of Heteromorphic SI | 297 |
| 14.5 The <i>Primula S</i> -locus | 297 |
| 14.5.1 Genetic Structure | 297 |
| 14.5.2 Location and Size of the <i>S</i> -locus | 301 |
| 14.5.3 Allelic Dominance | 301 |
| 14.6 Floral Development | 302 |
| 14.7 Molecular Genetic Characterisation of the <i>Primula S</i> -locus: Current Status | 303 |
| 14.8 Conclusions and Future Prospects | 305 |
| References | 306 |
| | |
| Index | 309 |