

Reproductive Biology of Angiosperms

The science of understanding plant reproduction is more than four hundred years old. Today, with integration of molecular biological tools, plant reproductive biology has catapulted into an exciting field of research. It has become an integral part of evolutionary biology, conservation biology, climate change studies, population biology, genetics, horticulture and many more fields. Considering the widening scope of plant reproductive biology, this book focusses on teaching the core concepts of plant reproduction supplemented with latest findings in the field. Uniquely, this book addresses both theoretical and practical perspectives by providing easy protocols of experiments related to the content of each chapter, thus, making the book useful for an entire spectrum of students, teachers and researchers.

The content of the book is designed for the undergraduate syllabi of embryology, reproductive biology of flowering plants, reproductive ecology of flowering plants, and plant breeding, taught in universities across the country. The content is well-supplemented with photographs and illustrations to enhance the understanding of the structures and processes involved in plant reproduction. Interesting information, which may incite the curiosity of learners, appears at appropriate places in the narrative in a box format. Detailed comparisons of similar/related concepts which commonly are difficult to comprehend for first-time learners are especially brought out in the text. The key concepts are revisited at the end of each chapter in the form of glossary. Practice questions at the end of each chapter have been added as part of pedagogical approach of conceptual learning. To help readers develop a complete understanding of the subject, step-by-step description of experiments related to the content are also provided.

Yash Mangla is Assistant Professor in the Department of Botany at Acharya Narendra Dev College, University of Delhi. His specialization is developmental, molecular, and reproductive biology of angiosperms.

Priyanka Khanduri is Assistant Professor in the Department of Botany at Vidyasagar Metropolitan College, University of Calcutta. Her research interests include developmental and reproductive biology of angiosperms, and phylogenetics.

Charu Khosla Gupta is Professor of Botany at Acharya Narendra Dev College, University of Delhi, with teaching and research experience spanning 24 years. She specializes in reproductive biology of angiosperms. She is the recipient of Teaching Excellence Award for innovation (2015) from the University of Delhi and Meritorious Teacher Award (2020) from the Directorate of Higher Education, Government of NCT of Delhi.



Reproductive Biology of Angiosperms Concepts and Laboratory Methods

Yash Mangla Priyanka Khanduri Charu Khosla Gupta





CAMBRIDGE UNIVERSITY PRESS

University Printing House, Cambridge CB2 8BS, United Kingdom

One Liberty Plaza, 20th Floor, New York, NY 10006, USA

477 Williamstown Road, Port Melbourne, VIC 3207, Australia

314-321, 3rd Floor, Plot 3, Splendor Forum, Jasola District Centre, New Delhi-110025, India

103 Penang Road, #05-06/07, Visioncrest Commercial, Singapore 238467

Cambridge University Press is part of the University of Cambridge.

It furthers the University's mission by disseminating knowledge in the pursuit of education, learning and research at the highest international levels of excellence.

www.cambridge.org

Information on this title: www.cambridge.org/9781009160407

© Yash Mangla, Priyanka Khanduri and Charu Khosla Gupta 2022

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 2022

Printed in India

Library of Congress Cataloging-in-Publication Data

Names: Mangla, Yash, author. | Khanduri, Priyanka, author. | Khosla, Charu, author.

Title: Reproductive biology of angiosperms: concepts and laboratory methods / Yash Mangla, Priyanka Khanduri, Charu Khosla Gupta

Description: New York, NY: Cambridge University Press, 2022. | Includes bibliographical references and index.

Identifiers: LCCN 2021055613 (print) | LCCN 2021055614 (ebook) | ISBN 9781009160407 (paperback) | ISBN 9781009160414 (ebook)

Subjects: LCSH: Angiosperms—Reproduction.

Classification: LCC QK495.A1 M35 2022 (print) | LCC QK495.A1 (ebook) | DDC 583-dc23/eng/20211221

LC record available at https://lccn.loc.gov/2021055613

LC ebook record available at https://lccn.loc.gov/2021055614

ISBN 978-1-009-16040-7 Paperback

Cambridge University Press has no responsibility for the persistence or accuracy of URLs for external or third-party internet websites referred to in this publication, and does not guarantee that any content on such websites is, or will remain, accurate or appropriate.



To Our Gurus ...
Our Constant Source of Inspiration



Contents

Foreword		XVII
Preface		xxi
Acknowled	gments	xxiii
Image Sour	ces	xxv
Chapter 1.	An Introduction to the Reproductive Biology of Flowering Plants	1
1.1	Different Aspects of Reproductive Biology of Flowering Plants	1
1.2	Scope of Reproductive Biology of Angiosperms	5
Chapter 2.	The Flower	9
2.1	Introduction	9
2.2	Organization of a Flower	11
2.3	Sexual Diversity in Angiosperms	14
2.4	Origin of Flower	16
2.5	Induction of Flowering	18
2.6	ABCDE Model of Floral Organ Development	18
	Glossary	20
	Key Questions	21
Pra	cticals	
	Exercise 2.1: To study important morphological features of randomly selected flowers	21
	Exercise 2.2: To observe the sexuality of randomly selected flowers	23
Chapter 3.	Brief Historical Account on Transformation of Classical Embryology	
-	to Integrated Reproductive Biology	25
3.1	Early Discoveries	25
3.2	Era of Exploration	26
3.3	Years that Laid the Foundation	27
3.4	Broadening Horizons	30
3.5	Integration of Ecological, Evolutionary and Genetical Approaches to the Study of Plant Reproductive Systems	35
Chapter 4.	The Anther and Male Gametophyte	40
4.1	Introduction	40
4.2	Anther Structure and Development	41



		Contents
4.2.1	I Structure	41
4.2.2	2 Development	42
	4.2.2.1 Phase I	43
	4.2.2.2 Phase II	45
4.3 Antl	her Wall Layers	45
4.3.1	Epidermis	46
4.3.2	2 Endothecium	48
4.3.3	B Middle Layers	51
4.3.4	4 Tapetum	52
4.4 Antl	her Dehiscence	57
4.5 Polle	en Development	60
4.5.1	Microsporogenesis	60
	4.5.1.1 Cytokinesis during Microsporogenesis	64
	4.5.1.2 Role of Callose during Microsporogenesis	66
4.5.2	2 Microgametogenesis	66
	4.5.2.1 Vegetative and Generative cell	68
	4.5.2.2 Bi- and Tri-cellular Pollen Grains	69
4.6 Male	e Germ Unit (MGU)	71
4.6.1	Structure	72
4.6.2	2 Functions	72
4.6.3	3 Sperm Dimorphism	74
4.7 Polle	en Wall: Structure, Synthesis and Features	74
4.7.1	Pollen Wall Structure	75
4.7.2	Pollen Wall Synthesis	75
4.7.3	Pollen Coat Substances	80
4.8 Cha	racteristics of Pollen	81
4.8.1	Pollen Dispersal Unit	82
4.8.2	Pollen Aperture	85
4.8.3	B Pollen Polarity	87
4.8.4	4 Pollen Symmetry	88
4.8.5	5 Pollen Shape	88
4.9 NPC	C System	88
4.10 Nem	nec Phenomenon	89
4.11 Polle	en Development and Metabolism	91
Glos	ssary	93
Key	Questions	95
Practical	s	
Exer	cise 4.1: To study anther wall layers and microsporogenesis	96
Exer	cise 4.2: To study a mature anther and its dehiscence	97
Exer	cise 4.3: To study the ultrastructure of pollen wall layers using	
	transmission electron micrograph	100



Contents

Cambridge University Press & Assessment 978-1-009-16040-7 — Reproductive Biology of Angiosperms Yash Mangla , Charu Khosla Gupta , Priyanka Khanduri Frontmatter More Information

> Exercise 4.4: To identify the cellular stage of pollen at the time of anther dehiscence 100 Exercise 4.5: To study the ultrastructure of male germ unit 102 Exercise 4.6: To test the pollen grain fertility and viability 103 Exercise 4.7: To estimate the production of pollen grains in a flower 107 Exercise 4.8: To study the morphological features (shape, exine pattern and aperture) of pollen grains of different species 108 Chapter 5. The Ovule and Female Gametophyte 119 5.1 Introduction 119 5.2 Basic Structure of Ovule 120 5.3 Development of Ovule 121 5.4 Ovule Diversity 122 5.4.1 Types of Ovule on the Basis of Degree of Curvature 122 5.4.2 Types of Ovule on the Basis of Thickness of Nucellus 126 5.5 Structures Associated with Ovules 127 5.6 Development of Female Gametophyte 131 5.6.1 Megasporogenesis 132 5.6.2 Selection of Functional Megaspore and Types of Embryo Sac Development 132 5.6.3 Megagametogenesis 136 5.6.4 Different Types of Embryo Sac 138 5.6.4.1 Monosporic Embryo Sacs 138 5.6.4.2 Bisporic Embryo Sacs 139 5.6.4.3 Tetrasporic Embryo Sacs 140 5.6.4.4 Embryo Sac Development in Chrysanthemum cinerariaefolium 143 5.7 Cellular Anatomy and Ultrastructure of Cells of Embryo Sac 144 5.7.1 Egg Cell 145 5.7.2 Synergids 147 5.7.3 Central Cell 150 5.7.4 Antipodal Cells 150 5.8 Unique Ovules and Embryo Sacs 151

Glossary

Practicals

Key Questions

Exercise 5.1: To study different types of ovules

Exercise 5.2: To study special ovular structures

embryo sac development

Exercise 5.6: To estimate number of ovules in a flower

Exercise 5.3: To study monosporic, bisporic and tetrasporic types of

Exercise 5.4: To study Polygonum-type of embryo sac development

Exercise 5.5: To study the ultrastructure of egg cell, synergids and central cell

Exercise 5.7: To assess the receptivity of ovules using Toluidine Blue 'O' test

153

154

155

158

159

163

164

166

168

ix



X			Contents
Chapter 6.	Pollin	ation	174
6.1	Introd	luction	174
6.2	Types	of Pollination: Self and Cross	175
	6.2.1	Self-Pollination	176
	6.2.2	Cross-Pollination	177
6.3	Mecha	anisms to Promote Cross-Pollination	179
6.4	Modes	s of Pollination	181
6.5	Abioti	c Pollination	182
	6.5.1	Pollination by Wind: Anemophily	182
	6.5.2	Pollination by Water: Hydrophily	185
6.6	Biotic	Pollination	188
	6.6.1	Pollination by Insects: Entomophily	188
		6.6.1.1 Bee and Wasp Pollination	189
		6.6.1.2 Fly Pollination	191
		6.6.1.3 Ant Pollination	192
		6.6.1.4 Butterfly Pollination	192
		6.6.1.5 Moth Pollination	193
		6.6.1.6 Beetle Pollination	195
	6.6.2	Pollination by Birds: Ornithophily	195
	6.6.3	Pollination by Bats: Chiropterophily	198
	6.6.4	Pollination by Snail: Malacophily	198
	6.6.5	Some Unusual Pollinators	199
6.7	Ambo	phily	202
6.8	Pollen	Storage	202
	6.8.1	Methods of Pollen Storage	203
	6.8.2	Utility of Pollen Storage: Some Examples	204
	Glossa	nry	205
	Key Q	uestions	205
Pra	cticals		
	Exerci	se 6.1: To study the time of anther dehiscence	206
	Exerci	se 6.2: To study the histochemistry of floral rewards	207
	Exerci	se 6.3: To study the floral features of various species and discuss them i	n
		context of pollination syndrome	211
Chapter 7.	Pollen	-Pistil Interactions and Fertilization	216
7.1	Introd	luction	216
7.2	Stigma	a and Style	217
7.3	Pollen	-Pistil Interactions	221
	7.3.1	Pollen Capture and Adhesion	222
	7.3.2	Pollen Hydration	225
	7.3.3	Pollen Germination	225
	7.3.4	Penetration of Stigma by Pollen Tube	226



Contents		xi
	7.3.5 Pollen Tube Growth	227
	7.3.5.1 Pollen Tube Cytoplasm	227
	7.3.5.2 Pollen Tube Wall	229
7.4	Pollen Tube Guidance: Cues from Sporophytic Tissue,	
,,,	Stylar Exudates and Ovule	231
7.5	Pollen Tube Entry into Ovule and Embryo Sac	233
7.6	Double Fertilization	233
7.7	Unique Cases	236
7.8	<i>In vitro</i> Pollen Tube Germination	240
	Glossary	242
	Key Questions	243
Pra	cticals	
	Exercise 7.1: To study the stigma and the styles of different flowers	244
	Exercise 7.2: To study the stigma receptivity by cytochemical localization of	
	non-specific esterases and peroxidase activity	244
	Exercise 7.3: To test germinability of pollen grains under <i>in vitro</i> condition	2.45
	through various methods	247
	Exercise 7.4: To study the pollen tube path in the pistil by decolorized aniline blue staining	249
Chapter 8.	Self-Incompatibility	257
8.1		257
8.2	Self-incompatibility: Classification and Types	258
	Genetic Control of Self-incompatibility	259
	8.3.1 Homomorphic Self-incompatibility	259
	8.3.1.1 Gametophytic Self-incompatibility (GSI)	260
	8.3.1.2 Sporophytic Self-incompatibility (SSI)	261
	8.3.2 Two-loci or Bi-factorial System	262
	8.3.3 Heteromorphic Self-incompatibility	262
8.4	Pollen and Pollen Tube Rejection	264
	8.4.1 Homomorphic Systems	264
	8.4.1.1 Sporophytic Self-incompatibility System	265
	8.4.1.2 Gametophytic Self-incompatibility System	267
	8.4.2 Heteromorphic Systems	271
8.5	Methods to Overcome Self-incompatibility	273
	8.5.1 Mixed Pollination	273
	8.5.2 Bud Pollination	273
	8.5.3 Stub Pollination	274
	8.5.4 Intra Ovarian Pollination	274
	8.5.5 <i>In vitro</i> Pollination and Fertilization	275
	8.5.6 Modification of Stigmatic Surface	275
	8.5.7 Heat Treatment of Style	275



xii			Contents
	8.5.8	Irradiation	276
	8.5.9	Increased Level of Carbon Dioxide	276
	8.5.10	Parasexual Hybridization	276
	8.5.11	Genome Editing	277
	Glossa	ту	277
	Key Qu	estions	278
Pra	cticals		
	Exercis	e 8.1: To To determine the interspecific incompatibility in species using semi <i>in vivo</i> pollination and decolorized aniline blue staining method	279
	Exercis	e 8.2: To determine the type of homomorphic self-incompatibility (GSI or SSI) in a species by employing semi <i>in vivo</i> pollination and decolorized aniline blue staining method	281
	Exercis	e 8.3: To determine the mating/breeding system of a species using <i>in vivo</i> manual pollination	282
	Exercis	e 8.4: To calculate Index of Self-incompatibility (ISI)	284
	Exercis	e 8.5: To analyze the breeding system of a species by calculating its Pollen: Ovule ratio	285
Chapter 9.	Endost	perm	289
-	Introdu		289
		ructural Changes in the Central Cell and Formation of	
		y Endosperm Nucleus	290
9.3	Types o	of Endosperm	292
	9.3.1	Nuclear Endosperm	293
	9.3.2	Cellular Endosperm	297
	9.3.3	Helobial Endosperm	300
9.4	Some U	Jnusual Types of Endosperm	302
	9.4.1	Composite Endosperm	302
	9.4.2	Ruminate Endosperm	302
9.5	Cellularization of Nuclear Endosperm		303
9.6	Endosperm in Cereals		306
9.7	Hormo	nal Regulation of Endosperm	312
9.8	Function	ons of Endosperm	313
	9.8.1	Nutrition of Embryo	313
	9.8.2	Regulation of Embryo Development	313
	9.8.3	Seed Development	314
	9.8.4	Seed Germination	315
9.9	Nutriti	ve Tissues other than Endosperm	315
	9.9.1	Pseudoembryo Sac/Nucellar Plasmodium	315
	9.9.2	Perisperm	316
	9.9.3	Chalazosperm	317



Contents	xiii
Glossary	317
Key Questions	318
Practicals	010
Exercise 9.1: To dissect and study free-nuclear type of endosperm	
from developing seeds	319
Chapter 10. Zygotic Embryogenesis	324
10.1 Introduction	324
10.2 Structure of the Embryo	324
10.3 Egg to Zygote: Post-Fertilization Changes, Ultrastructure and Polarity	325
10.4 Embryogeny: From Zygote to Multi-cellular Embryo	327
10.4.1 Types of Embryo Development	328
10.4.2 Early Embryogenesis: Octant Configurations of Pro-embryo	329
10.5 Embryogenesis and Embryo Patterning	332
10.5.1 Embryogenesis and Embryo Pattern Formation in Dicots	332
10.5.2 Embryogenesis in Monocots	334
10.5.3 Embryogenesis in Poaceae	339
10.6 Unusual Features of Embryo and Embryogenesis in Some Angiosperms	340
10.6.1 Embryo Development in <i>Paeonia</i>	341
10.6.2 Reduced Embryos	341
10.7 Suspensor	342
10.7.1 Structure	342
10.7.2 Ultrastructure	344
10.7.3 Role of Suspensor	345
10.8 Embryo Nourishment	347
Glossary	349
Key Questions	349
Practicals	
Exercise 10.1: To study zygotic embryogenesis in dicots using micrographs	350
Exercise 10.2: To dissect young embryo from developing seed	351
Chapter 11. Polyembryony and Apomixis	357
11.1 Introduction	357
11.2 Polyembryony	359
11.2.1 Cleavage of Zygote or Proembryos	359
11.2.2 Formation of Embryos from Cells of Embryo Sac other than Egg Cell	360
11.2.3 Presence of More than One Embryo Sac within Same Ovule	361
11.2.4 Formation of Embryos by Sporophytic Tissue of Ovule	361
11.3 Classification of Polyembryony	363
11.4 Causes and Inheritance of Polyembryony	364
11.5 Practical Applications and Significance of Polyembryony	365
11.6 Apomixis	365



xiv	c	ontents
11.7	Types of Apomixis	366
	11.7.1 Sporophytic Apomixis	367
	11.7.2 Gametophytic Apomixis	367
	11.7.2.1 Diplospory	367
	11.7.2.2 Apospory	370
11.8	Role of Pollination in Embryo and Endosperm Development among Apomicts	373
	Genetics of Apomixis	373
	Potential Applications of Apomixis	375
	Methods to Screen and Study Apomixis	379
	Glossary	380
	Key Questions	381
Prac	cticals	
	Exercise 11.1: To screen apomixis in ovules using histo-clearing technique	382
	Exercise 11.2: To study the polyembryony in seeds	386
	Exercise 11.3: To determine the type of embryo by enumerating key features	387
Chapter 12	Seed	390
-	Introduction	390
	Structure and Morphology of Seeds	392
	Types of Seed	394
	12.3.1 Classification 1: Based on Ovule Type	394
	12.3.2 Classification 2: Based on Embryo Size, Shape and Position	395
	12.3.3 Other Types	396
12.4	Seed Coat	398
	12.4.1 Structure and Development	398
	12.4.2 Functions of Seed Coat	406
12.5	Specialized Seed Associated Structures/Appendages	409
	S Seed Dispersal	412
	12.6.1 Advantages of Dispersal	413
	12.6.2 Mechanisms of Dispersal	413
	12.6.2.1 Autochory	414
	12.6.2.2 Anemochory	417
	12.6.2.3 Hydrochory	418
	12.6.2.4 Zoochory	420
	Glossary	424
	Key Questions	425
Prac	cticals	
	Exercise 12.1: To calculate the mass and determine the shape (seed traits)	
	of different seeds	426
	Exercise 12.2: To classify different types of seeds	428
	Exercise 12.3: To study seed dispersal mechanisms in various species	428



Contents	XV
Exercise 12.4: To calculate percentage seed viability, germinability and seed vigor	428
Exercise 12.5: To calculate the ovule: seed ratio	431
Exercise 12.6: Observation of seed dispersal mechanism	432
Chapter 13. Plant Germline Transformation	436
13.1 Introduction	436
13.2 Plant Germline Transformation	437
13.3 Male Germline Transformation	439
13.3.1 Agrobacterium Mediated Transformation	442
13.3.2 Particle Bombardment Method	444
13.3.3 MAGELITR	444
13.3.4 Microinjection	445
13.3.5 Sonication	445
13.3.6 Electroporation	445
13.4 Female Germline Transformation	446
13.4.1 In Planta Agroinfiltration	447
13.4.2 Floral Dip	447
13.4.3 Floral Spray	448
13.4.4 Pollen Tube Mediated Transformation	449
13.4.5 Ovary/Pistil Drip Transformation	449
13.5 Factors Influencing Germline Transformation	450
Glossary	451
Key Questions	452
Practicals	
Exercise 13.1: To identify the uninucleate stage of pollen grains and demonstration of technique of anther culture	452
Exercise 13.2: To demonstrate the floral dip method of germline transformation	
Index	463
Color Plates	473



Foreword

Plants in general and flowering plants (angiosperms) in particular are the essential components for sustenance of life of all non-photosynthetic organisms on our planet. Plants reproduce by asexual as well as sexual means. Asexual reproduction is not congenial for long-term sustenance and evolutionary processes of the species because of genetic uniformity of the progeny. Sexual reproduction which permits genetic recombination is the dominant mode. Although Angiosperms were the last to evolve as land plants, they soon became the most successful and dominant group amongst land plants. Their success is largely due to the mode of their reproduction through the evolution of the flower and the consequent advantages it brought in. For human beings, flowering plants provide most of their essential needs - food, fibres, shelter, medicines, clean air and water. Reproduction is the basis for sustenance of any species. Thus, understanding reproductive biology of flowering plants is important not only from the fundamental point of view but also for their manipulation for human welfare. Reproductive biology of angiosperms is more complex when compared to other groups of plants because of the involvement of the flower. The progress in understanding the structural and functional aspects of reproduction has been very slow.

Initial studies on reproductive biology of angiosperms were largely confined to examining embryological details using fixed and sectioned materials. Enormous data accumulated over the years on the developmental details of the pollen grains, ovules and female gametophyte, double fertilization, embryo and endosperm, seed and fruit development. These advances were taught to the undergraduate and postgraduate students under the title embryology of angiosperms as a part of their curriculum. Following the development of electron microscopy and histochemistry, embryological details were further elaborated by using these techniques. Development of aseptic culture techniques broadened scope for experimental studies on embryological processes leading to a slow but steady understanding of the functional details of embryological structures. These developments were incorporated in some of the books of embryology under a chapter on experimental embryology. However, there was hardly any integrated account of embryological processes in relation to the structure with their function. Pre-fertilization aspects of reproductive biology covering the details of pollen, pistil, and pollen-pistil interactions, which are unique to angiosperms and play a critical role in their successful evolution, were the last to enter the field of embryology of angiosperm. Surprisingly, pollination on which plenty of literature has long been available and which is a critical requirement for angiosperm reproduction was not a part of embryology.



xviii Foreword

Now enormous data has accumulated on all aspects of reproductive biology of angiosperms through interdisciplinary studies and it is high time to teach this subject as "Reproductive Biology" (rather than embryology) integrating all these advances starting with flower development until fruit and seed maturation and their dispersal.

Continued research and teaching of reproductive biology of angiosperms has become highly relevant in the light of human-induced environmental changes (intensification of agriculture, habitat loss and degradation, overexploitation of bio-resources, introduction of alien species and climate change) in recent decades and their impact on the sustenance of biodiversity and crop productivity. Human activities have not only accelerated extinction of species but also have pushed a large number of species to endangered status leading to the sixth mass extinction crisis. In the absence of effective remedial measures, a large proportion of biodiversity is likely to become extinct by the end of this century. Therefore, conservation of biodiversity is likely to become one of the most important agendas of the world in the coming decades. Reproduction is the basis for the sustenance of any species. In flowering plants, recruitment of new individuals which is the final step in a series of sequential reproductive events is the basis of species sustenance. Environmental changes have induced severe constraints on many reproductive events, particularly pollination and seed dispersal, leading to recruitment constraint. For any effective conservation of angiosperm species, it is important to understand reproductive biology of endangered species to identify reproductive and/or recruitment constraints and to apply effective measures to overcome such constraints. Plant conservation attempts so far, particularly in developing countries, have not been very successful; one of the reasons being our ignorance of the reproductive biology of the species to be conserved. Knowledge about reproductive biology is important not only for effective conservation but also to monitor the success of conservation measures.

Present book, Reproductive Biology of Angiosperms: Concepts and Laboratory Methods, by Yash Mangla, Priyanka Khanduri and Charu Khosla Gupta is going to be an important contribution to the field. It begins with a brief introduction that gives an account of different aspects of reproductive biology and highlights the importance of the subject to other areas of plant biology such as conservation biology, crop production, and evolutionary biology. Historical account, that comes next, elaborates briefly the development of "classical embryology" through various stages into an integrated discipline of "reproductive biology" and highlights the contributions of several well-recognized investigators. Various chapters starting from the flower until seed dispersal give a reasonably comprehensive account of different aspects of reproductive biology. A chapter on genetic transformation is also included at the end. The book is illustrated with photographs and diagrammatic sketches of high quality.

An attempt is made in all the chapters to give an integrated account of reproductive structures (as revealed through light and electron microscopy) and their functions. The deep understanding involved was realized through the application of the techniques from different disciplines such as histochemistry, physiology, biochemistry, molecular biology, and evolutionary biology. Such an integrated account is hardly given in any of the existing books in this field. Boxes and tables have been used profusely to provide clarity on many



Foreword xix

aspects. Glossary of a large number of technical terms and key questions are given at the end of each chapter. The details of the practical exercises given for each chapter are going to be very useful for the teachers as well as students. To my knowledge there is no such book available so far in this field. The present book is thus a very welcome addition to the literature on reproductive biology of angiosperms. I congratulate the authors for compiling such a book. I am confident that the volume is going to be very useful not only for teachers and students of Reproductive Biology but also those interested in any aspect of reproduction of angiosperms.

K. R. Shivanna (Former Professor and Head, Department Botany, University of Delhi) INSA Honorary Scientist Ashoka Trust for Research in Ecology and the Environment, Bengaluru, India



Preface

The inception of interest in understanding mechanisms of plant reproduction is as old as inception of interest in biology. The seminal work and critical observations by Charles Darwin can be regarded as a foundation for establishing a wide interest in pollinators and reproductive biology of angiosperms as a formal subject. In the last few decades, systematic field investigations, advancement of microscopy tools, and molecular techniques have taken the reproductive biology of angiosperms to a new zenith. The scope of the subject is no longer limited to just studying embryo-endosperm development and taxonomic studies but is extended to study the effect of climate change, evolution, conservation of threatened taxa, raising commercial plantations and orchards, pollinator management, seed development, population biology, phyto-geography, and much more. The reproductive biological studies are also closely linked with the understanding of, physiology, genetics and epigenetics of plants.

For a thorough understanding of the subject, a textbook summarizing the basic concepts of plant reproduction integrated with current research, is the need of the hour for both students and instructors. The aim of the present book is to provide a comprehensive account of basic concepts and recent developments in the field of reproductive biology of flowering plants with essential practical exercises. The book extensively covers all the topics from structure of a flower to seed dispersal and presents the concepts with accompanying color photographs and illustrations wherever necessary, to enhance the level of a student's perception. The new, advanced and interesting information is also provided in a box format in each chapter to reinforce learning. An elaborate glossary and questions are provided with each chapter for quick revision and concept enhancement. Boxes summarizing differences between two terms/concepts which students otherwise usually find difficult to comprehend have also been furnished in the book. This book is a blend of theoretical concepts and details of hands-on exercises in the field and laboratory. Methods for field observations, sample observation tables, and suggestions for plant materials to be used for classroom studies/demonstrations pertaining to each concept have also been provided. In addition, the observation sections under practicals are supplemented with the photographs. This should surely help the instructors to demonstrate and students to grasp the concept effectively

The current book has been specially structured keeping in mind the syllabi of the leading universities in the country. The content is all inclusive of different curricula frameworks implemented by the University Grants Commission across the universities. It can be used



xxii Preface

as a text book as well as a reference book by both graduate and undergraduate students along with researchers in the field. The glossary of technical terms at the end of each chapter should help students for quick revision for their competitive and entrance examinations. We hope the present edition of the book will certainly turn into a knowledge resource for the young minds and learners in the field.



Acknowledgments

We want to thank all those related directly or indirectly to this book. We dedicate this book to our mentors Late Professor H. Y. Mohan Ram, Professor K. R. Shivanna and Professor Rajesh Tandon who have been a constant source of inspiration and motivation for all three of us. We hold a deep sense of gratitude and reverence towards them. We are also thankful to Professor S. C. H. Barrett and Professor Odair José Garcia de Almeida for readily providing us with some wonderful photographs. We are equally indebted to all the researchers in the field of reproductive biology who supplemented our effort by providing illustrations and photographs from their original research. Our friends from the botany fraternity, Dr. P. Chitralekha, Dr. Sudip Kumar Roy, Dr. Chandan Barman, Dr. Vineet Kumar Singh, Mr. Arjun Adit, and Mr. Ashish Jangam very graciously shared their research work for which we are deeply obliged. We are also thankful to the International Association of Sexual Plant Reproduction Research (IASPRR) and the University of Wisconsin, Stevens Biology Lab for consenting to our use of images from their work. The permissions to use images from the Copyright Clearance Centre, Indian National Science Academy, Indian Academy of Sciences, Phytomorphology, Journal of Indian Botanical Society, Brazilian Journal of Botany and various journals have been invaluable and duly acknowledged. Our thanks are also due to all the creators whose work (text, figures, and illustrations) licensed under Creative Commons and free and open access journals, has been used in this book. The impetus for writing and publishing this book provided by Professor Ravi Toteja, Officiating Principal Acharya Narendra Dev College, University of Delhi and Dr. Ram Swarup Gangopadhyay, Principal, Vidyasagar Metropolitan College, University of Calcutta is deeply appreciated. Professor Toteja was also kind enough to run the plagiarism checks for our chapters. Hence, we take this opportunity to thank him and the University of Delhi for providing access to plagiarism software "Urkund", which helped immensely in making the content original. We are also thankful to the anonymous reviewers for their constructive comments and suggestions which encouraged us to not skip even the minutest details of the subject.

We are indebted to Dr. Vaishali Thapliyal, Senior Commissioning Editor at Cambridge University Press, for helping us bring out this comprehensive volume. She has been instrumental right from inception of proposal till its printing. Support provided by Cambridge University Press and staff members, especially Mr. Aniruddha De and Mr. Vikash Tiwari, is duly recognized.

Last but not the least we really thank our families and friends who supported us in this herculean venture.



Image Sources

Chapter 2

Figure 2.1 A. *Ranunculus*: 'Renoncules sauvages Bouton-d'or (Ranunculus acris)' by Giancarlo – Foto 4U is licensed under CC BY 2.0.

H. *Fuchsia* sp.: Arjun Adit, Research Scholar, Department of Botany, University of Delhi. U. *Yucca* sp.: Hemant Bisht.

V. *Cynotis* sp.: Ashish Jangam, Research Scholar, Department of Botany, Kolhapur University. *Figure 2.4* A and *Figure 2.5* B. *Phalaenopsis*, *Anthurium* sp. respectively: Arjun Adit, Research Scholar, Department of Botany, University of Delhi.

Figure 2.6 B and F. *Solanum* sp., *Ricinus communis*: Arjun Adit, Research Scholar, Department of Botany, University of Delhi.

C. Dianthus sp.: Hemant Bisht.

Chapter 3

Rudolf Jakob Camerarius, German botanist, 1665–1721. Artist unknown: http://www.biologie.uni-hamburg.de/b-online/e08/08.htm, Wikipedia public domain.

Josef Gottlieb Koelreuter: Wikipedia public domain.

Charles Darwin: By unknown author, originally published in *The Hornet* magazine; this image is available on University College London Digital Collections (18886), Public Domain, https://commons.wikimedia.org/w/index.php?curid=23436.

Amici: By Michele Gordigiani, http://catalogo.museogalileo.it/galleria/RitrattoGiovanni BattistaAmiciDepGAMFirenze.html, Public Domain, https://commons.wikimedia.org/w/index.php?curid=16010822.

Strasburger: By unknown; published in Munich. by J.F. Lehmann, http://ihm.nlm. nih.gov/images/B22559, Public Domain, https://commons.wikimedia.org/w/index. php?curid=18716986.

William Hofmeister: By Universitätsbibliothek Heidelberg, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=71111381.

Sergei Navashin: http://molbiol.ru/forums/index.php?showtopic=105009.

P. Maheshwari, BM Johri, SC Maheshwari, HY Mohan Ram, NS Rangaswamy: Indian National Science Academy, New Delhi.

Professor KR Shivanna: Professor KR Shivanna.



xxvi Image Sources

Chapter 4

Figure 4.1 B and *Figure 4.18*: University of Wisconsin-Stevens Biology Lab and IASPRR. *Figure 4.5* B: Dr Arun Kumar Mourya, Assistant Professor, Multanimal Modi College, Modinagar, Uttar Pradesh.

Parts of *Figure 4.15*, *4.16* and *4.23*: Halbritter et al. 2018.

Chapter 5

Figure 5.22 A–E: University of Wisconsin, Stevens Biology Lab.

F: https://commons.wikimedia.org/wiki/File:Lilium_embryo_4_nuclei.jpg.

Figure 5.19 A–C: Professor Odair José Garcia de Almeida, UNESP – Universidade Estadual Paulista, IB/Campus do Litoral Paulista.

Chapter 6

Figure 6.3 B. *Gloriosa superba*: Dr Rajesh Chaudhary, Associate Professor, Department of Biomedical Sciences, Acharya Narendra Dev College, University of Delhi.

Figure 6.8 D. Moth pollination: Dr Chandan Barman, Assistant Professor, Department of Botany, University of Gaur Banga, Malda, West Bengal.

Figure 6.10. Bat pollination: Dr Sudip Kumar Roy, Assistant Professor, Department of Botany, Charuchandra College Kolkata, West Bengal.

Figure 6.11. Snail pollination: Professor Rajesh Tandon, Professor, Department of Botany, University of Delhi.

Chapter 7

Figure 6.3 C. Dr Chandan Barman, Assistant Professor, Department of Botany, University of Gaur Banga, Malda, West Bengal.

F. Dr Vineet Kumar Singh, Assistant Professor, Department of Botany, Acharya Narendra Dev College, University of Delhi.

Chapter 8

Figure 8.1 B. Tristyly in *Lythrum salicaria*: Professor SCH Barrett, Professor Emeritus, University of Toronto, Canada.

Figure 7.8 C. Self-pollinated stigma showing deposition of callose on stigma and pollen tubes: Professor Rajesh Tandon, Professor, Department of Botany, University of Delhi.

Chapter 9

Figure 9.19: Dr P. Chitralekha, Associate Professor, Department of Botany, Dyal Singh College, University of Delhi.



Image Sources xxvii

Chapter 10

Figure 10.17: University of Wisconsin, Stevens Biology Lab.

Chapter 12

Figure 12. 1 A: 'Lodoicea maldivica. Coco de mer. Half used by locals for boat balers' by Mary Gillham Archive Project is licensed under CC BY 2.0, https://search.creativecommons.org/photos/d2a16ded-66bf-4fc5-b7b3-3376af3eff6f.

B: Arjun Adit, Research Scholar, Department of Botany, University of Delhi.

Figure 12.9 B: 'Magnolia Arils' by Editor B is licensed under CC BY 2.0, https://search.creativecommons.org/photos/e92bcbf9-77a9-4087-801e-fed2c8a3aae6.

D. Oil palm: Operculum: Professor S. Natesan, Tamil Nadu Agricultural University.

F: 'Nutmeg' by Giselleai is licensed under CC BY 2.0, https://search.creativecommons.org/photos/493b35d8-b8b3-49dc-951a-69a4c05ea66a.

I: 'Acacia tetragonophylla open seed pods' by John Tann is licensed under CC BY 2.0, https://search.creativecommons.org/photos/0907e44e-dfef-4bca-964e-60d1e8f151c6.

'Acacia tetragonophylla seeds' by John Tann is licensed under CC BY 2.0, https://search.creativecommons.org/search?q=Acacia%20tetragonophylla%20 seeds&license=by&license_type=commercial.

Figure 12.11 B: 'File:Alsomitra macrocarpa seed (syn. Zanonia macrocarpa).jpg' by Scott Zona from Miami, Florida, USA, is licensed under CC BY 2.0, https://search.creativecommons.org/photos/3b0545dd-7586-4a25-8112-e81b1a894374.

C: Dr. Sudip Kumar Roy, Assistant Professor, Department of Botany, Charuchandra College Kolkata, West Bengal.

F: 'Poppycock' by Jenny Downing is licensed under CC BY 2.0, https://search.creativecommons.org/photos/ac555fb7-107c-46bc-b00f-6727ddeab3b6.

Figure 12.12 A: COCONut 'Dauin beach' by bortescristian is licensed under CC BY 2.0, https://search.creativecommons.org/photos/ceebca24-633a-430e-a57d-38bed0eca5a9.

B: *Encyclopædia Britannica*, https://www.britannica.com/plant/coconut-palm/images-videos#/media/1/123794/238237.

C: *Encyclopædia Britannica*, https://www.britannica.com/science/seed-plant-reproductive-part/Dispersal-by-water#/media/1/532368/217444.

D: 'Lotus seed / 蓮の実(はすのみ)' by TANAKA Juuyoh (田中十洋) is licensed under CC BY 2.0,

https://search.creativecommons.org/photos/8ac504c4-8475-4614-8a9a-b62bc26525b6.

Figure 12.14 A: Winter berries by qmnonic is licensed under CC BY 2.0, https://search.creativecommons.org/photos/04fb465e-d1db-4562-9267-31593a0719f3.

B: *Encyclopædia Britannica*, https://www.britannica.com/science/seed-plant-reproductive-part/Dispersal-by-animals#/media/1/532368/155752.

C: Novemberry by Wildlife Terry is marked with CC0 1.0, https://search.creativecommons.org/photos/fbee2f01-41cb-471b-8b76-04dbd91f30bb.

D: King of the Stump by Peter G Trimming is licensed under CC BY 2.0, https://search.creativecommons.org/photos/4d61cec8-9286-4d9c-9bae-b7e28f378e41.