

Preface

SECTION I INTRODUCTION

1 The Evolution of Flowers

1.1 The origin of flowering plants

7 Integrating the Arabidopsis thatiana Flower, Induction Pathways and

Active the frent to their the the Stand to Main and the Main and the stand

7.1 Integrating the flowering-time patheory hollog shold 5.51

a Shick at he water all he have a too de the rogendo a

6.1 Physiological changes at the sholl aplication

- 8.4 Floral mension Ren

9. Development of the Horal Organs

- 1.2 Early reproductive structures
- 1.3 The first flowers
- 1.4 Floral diversification

2	Historical Interpretations of Flower Induction and Flower Development
	2.1 The foliar theory of the flower
	2.2 The foliar theory in an evolutionary context
	2.3 The transition to flowering
	2.4 Developmental explanations of floral induction
	2.5 Environmental explanations of floral induction
	2.6 The florigen problem
	10.1 Evolutionary hat SPAR WARDE BOX Banadriphon in tors

SECTION II THE MOLECULAR MECHANISMS OF FLOWERING: INDUCTION AND DEVELOPMENT

PART A Induction of Flowering

21

V

1

3

3

7

7

8

10

10

15

15

16

16

19

3	Flower Induction in Arabidopsis thaliana	25
	3.1 Arabidopsis thaliana as a model system for the study of flowering	25
	3.2 Flowering-time mutants	30
	17.2 Padilitation of philipping alon marphigms of T.I.	
4	The Autonomous Pathways for Floral Inhibition and Induction	35
	4.1 The floral inhibition pathway	35
	4.2 The autonomous induction pathway	39
	4.3 Other endogenous factors which influence flowering time	41
5	The Photoperiodic Pathway of Floral Induction	43
	5.1 Sensing daylight	43
	5.2 Measuring time	48
	5.3 Integrating light and clock signals	50
	18.2. What pollinatory signal against and granomatori NAT	
6	The Vernalization Pathway of Floral Induction and the Role of Gibberellin	52
	6.1 The vernalization promotion pathway	52



viii CONTENTS

- 6.2 The gibberellin promotion pathway 6.3 Does gibberellin act in the vernalization promotion pathway as well as independently?
- Integrating the Arabidopsis thaliana Flower Induction Pathways and 7 **Assessing the Extent to Which the Model Is Ubiquitous** 7.1 Integrating the flowering-time pathways 7.2 The Arabidopsis flowering-time model in other species

PART B Development of Flowers

8 Changes at the Shoot Apical Meristem in Response to Floral Induction 71 8.1 Physiological changes at the shoot apical meristem 71 8.2 Shoot apical meristem anatomy 72

	8.3 Gene expression patterns in the shoot apical meristem	73
	8.4 Floral meristem identity genes act downstream of the	
	flowering-time integrators	74
	8.5 Floral meristem identity genes	74
9	Development of the Floral Organs	83
	9.1 The original ABC model of flower development	83
	9.2 The role of D function genes	90
	9.3 The role of E function genes	90
	9.4 The role of cadastral genes	92
	9.5 The quartet model of organ identity*	94
10	The ABC Model in Evolution	95
	10.1 Evolutionary history of MADS box transcription factors	95
	10.2 ABC model in gymnosperms?	96
	10.3 ABC model in monocots?	98
	10.4 Variations on the ABC model	101
11	Function and Development of Gametophytes	103
	11.1 Alternation of generations in multicellular organisms	103
	11.2 The angiosperm female gametophyte	105
	11.3 The angiosperm male gametophyte	107
	11.4 Events following pollination	109
12	Preventing Self-fertilization	111
	12.1 Reducing self-pollination in a hermaphroditic flower	111
	12.2 Monoecy	113
	12.3 Dioecy	114
	12.4 Self-incompatibility (SI)	115
	12.5 Sporophytic self-incompatibility (SSI)	116
	12.6 Gametophytic self-incompatibility (GSI)	119
	12.7 Heteromorphic self-incompatibility	120
	The Alexandra Mana Participant of March 19 and 19 and the Contract of T	

56

58

59

59

64

69

CONTENTS ix

100 m

20

14.1.14

2

1. 2

SECTION	III P	OLLINATION SUCCESS: MOLECULAR AND ECOLOGICAL INTERACTIONS	123
PART A H	low a	and Why Does Floral Form Vary?	125
	13 V	Why Are Flowers Different? Pollination Syndromes—The Theory	127
		3.1 Cross pollination	127
		3.2 Abiotic pollen vectors	127
		3.3 Biotic pollen vectors	129
		3.4 Principles underlying the pollination syndrome concept	129
		3.5 The pollination syndromes	130
	14 C	hanging Floral Shape and Structure	138
	1	4.1 Changing corolla size	138
	1	4.2 Changing corolla symmetry	140
	1	4.3 Changing petal shape	143
	1	4.4 Generating a composite inflorescence	145
	15 C	olouring the Flower	147
	1	5.1 Colour as a signal	147
	1	5.2 Plant pigments	148
	1	5.3 Carotenoid synthesis	149
	1	5.4 Flavonoid synthesis	151
	1	5.5 Betalains	156
	16 E	nhancing Flower Colour	158
		6.1 Mixing pigments	158
	2.2	6.2 Co-pigmentation	158
		6.3 Regulation of pigment distribution	159
		6.4 The effects of metal ions	162
	1	6.5 The importance of pH	163
		6.6 The role of petal cell shape	165

PART B The Influence of Pollinators on Floral Form

 Inc monetec	 VIIIIACOID	

17	Are Flowers under Selective Pressure to Increase Pollinator Attention?	171
	17.1 Competition for pollinator attention	171
	17.2 Facilitation of pollination	172
	17.3 Techniques for investigating the role of pollinator attention in	
	limiting fitness	172
	17.4 Evidence based on fruit and seed set following hand pollination	175
	17.5 Evidence from mixed species plots	176
	17.6 Analysis of character traits potentially displaced by pollination	
	competition	177
18	Do Pollinators Discriminate between Different Floral Forms?	181
	18.1 What pollinators see	181
	18.2 What pollinators sense in other ways	183
	18.3 Discrimination between petals of different colours	184

x CONTENTS

18.4	Discrimination between corollas of different sizes
18.5	Discrimination between zygomorphic and actinomorphic flowers
18.6	Discrimination between flowers with different petal cell shapes
18.7	Discrimination between flowers on the basis of scent

19 Pollination Syndromes—The Evidence19.1 Historical context 19.2 Putting the assumptions together 19.3 Evidence for pollination syndromes 19.4 Evidence against pollination syndromes 19.5 The most effective pollinator?

Epilogue References

Index	223
 15.2 Fiant pigments 15.3 Canverged sentited 15.4 Flavonoid sentited 15.6 Betalaum 15.6 Betalaum 16.1 Mixing pigments 	
	96

17.1 Competition for bullication of blattest must bigge all 211		
17.3 Techniques for investigationindent politication to attain in		