

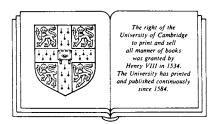
Patterns in plant development



Patterns in plant development

SECOND EDITION

Taylor A. Steeves
Ian M. Sussex



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Dedicated to
R. H. Wetmore
and to the memory of
C. W. Wardlaw



Contents

	Preface	xi
	Acknowledgments	xv
1.	Development in the vascular plants References/4	1
2.	Embryogenesis: beginnings of development Patterns of embryo development/6 Cellular changes during embryogenesis/20 General comment/24 References/25	6
3.	Analytical and experimental studies of embryo development The environment of the embryo/26 The role of the suspensor/36 The completion of embryogeny/39 General comment/41 References/44	26
4.	The structure of the shoot apex Morphology/47 Histology/47 General comment/59 References/60	46
5.	Analytical studies of the shoot apex Growth of the shoot apex/62 Distribution of cell division in the shoot apex/63 Cytohistological studies/70 Developmental changes in zonation/75 Clonal analysis/76 General comment/80 References/83	62
6.	Experimental investigations on the shoot apex Apical autonomy/86 Organization and integration in the shoot apex/91	86

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vii



vii		Contents
	General comment/97 References/98	
7.	Organogenesis in the shoot: leaf origin and position Leaf initiation and early development/101 Analysis of early leaf development/106 Questions of leaf development/108 Leaf position – phyllotaxy/109 General comment/121 References/122	100
8.	Organogenesis in the shoot: determination of leaves and branches Leaf determination/124 Dorsiventrality/134 Branching/135 General comment/144 References/145	124
9.	Organogenesis in the shoot: later stages of leaf development Development of fern leaves/147 Development of angiosperm leaves/150 Analysis of leaf development/160 General comment/172 References/174	147
10.	Determinate shoots: thorns and flowers Determinate meristems – thorns/176 Reproductive morphology/178 Development of the floral apex/179 Analysis of floral transformation/185 Experimental analysis of floral meristems/188 General comment/198 References/200	176
11.	The development of the shoot system Patterns of shoot expansion/203 Regulation of shoot expansion/208 Periodicity of shoot growth/214 The components of the shoot system/217 The ontogeny of the shoot system/218 Trees, shrubs, and herbs/224 General comment/225 References/226	203



Cor	ntents	— ix
12.	The root The root apex/232 Experimental investigation of root development/240 Root branching/245 Associations with microorganisms/248 General comment/250 References/252	229
13.	Differentiation of the plant body: the origin of pattern Genetic correlates of differentiation/255 Methods for the study of differentiation/259 Early stages of differentiation in roots/260 Early stages of differentiation in shoots/266 General comment/282 References/283	255
14.	Differentiation of the plant body: the elaboration of pattern Cellular changes during differentiation/285 Later stages of differentiation in roots/290 Later stages of differentiation in shoots/298 Experimental studies of vascular differentiation/301 General comment/307 References/309	285
15.	Secondary growth: the vascular cambium The initiation of cambial activity/311 The organization of the vascular cambium/313 The dynamic state of the cambium/318 Changing patterns in the cambium/325 The question of cambial initials/326 Terminology/329 General comment/329 References/331	311
16.	Secondary growth: experimental studies on the cambium Cambial initiation/333 Cambium cultures/335 The physical environment/336 Orientation in the cambium/340 General comment/345 References/346	333
17	. Alternative patterns of development Developmental potentialities of isolated cells/348	348



x	Contents
Plant regeneration/360	
General comment/367	
References/368	
Credits	371
Author index	377
Subject index	382



Preface

This volume is a revised edition of a book first published, under the same title, in 1972 and now several years out of print. In recognition of the impressive body of developmental research that has been reported since the publication of the original volume, this edition has been substantially modified and modestly enlarged. The point of view of the original, however, has been retained. It is, as the title implies, structural and organismal. We have attempted to document the developmental process as the plant undergoes it, beginning with the zygote and the formation of the embryo, continuing with the development of the primary body and completing the picture with a treatment of secondary growth. We have not, therefore, undertaken to analyze phenomena like cell growth, meristematic activity, or polarity as topics in themselves, although certain phenomena, notably differentiation and the potency of differentiated cells, have been given special treatment. It may be argued that this approach could fail to reveal fundamental generalizations about development. Nevertheless, our goal was to show how the plant develops as an organism and we have attempted to adhere to it.

In the more than fifteen years that have elapsed since the original edition was published, there have been phenomenal advances in the fields of cellular and molecular biology, and these discoveries are being applied with ever-increasing intensity to the interpretation of plant development. One may reasonably ask, therefore, whether the structural and organismal approach to development has become obsolete. The effort expended in revising this book signifies that our answer is emphatically "No." It is undeniably true that the enhanced understanding of processes at the cellular level is providing answers to developmental questions that seemed almost beyond our reach only a few years ago. It is equally true, however, that the fundamental developmental questions are posed by the formation of an integrated organism within which the multitudes of diverse cells occupy their places and perform their specific functions in the context of distinctive patterns. Indeed the events that occur at the cellular level reveal their developmental significance in the patterns within which they occur, that is, in the morphogenesis



xii — Preface

that forms a functioning organism. This essential point was well made more than one hundred years ago in the aphorism attributed to Anton deBary: "The plant forms cells, not cells the plant." Thus we believe that the explosion in molecular biology will achieve its most beneficial impact upon the understanding of development if it is based upon a profound appreciation of development at the organismal level.

On the other hand, we have not undertaken to give just a descriptive account of structural changes in development for such a treatment would grossly misrepresent the field of developmental morphology as it is today and has been for several decades. This field of investigation has become causal in its interpretations and experimental in its methods. Thus, while we have not attempted to analyze control mechanisms as physiological or biochemical processes, we have been very much concerned with them as they regulate developmental patterns. We have attempted as far as possible to limit the quantity of purely descriptive material by selecting particular examples that have been well documented and illustrated in published accounts and using them to present particular developmental patterns. The variability in pattern is then introduced briefly following the detailed account of the "type." We hope that this technique has enabled us to present sufficient detail for a meaningful picture without too great a burden of description. As in the earlier edition, we have found it necessary to limit the treatment to the vascular plants and thus, regrettably, to exclude significant work dealing with algae, fungi, and bryophytes.

In this revision much new material has been introduced. Wherever possible the exciting findings of molecular biology have been drawn upon to aid in the interpretation of morphogenetic events. This is particularly evident in the account of the embryonic phase of development. Substantial reference has been made to the application of the technique of clonal analysis, which, although not new, has only lately been recognized as a powerful tool in the difficult task of tracing cell lineages in plants. At the same time it is recognized that plant morphologists have made major strides in interpreting the organization of whole plants, particularly those of large stature, and the developmental significance of architectural analysis is stressed in this edition.

This book is intended to be an introduction to plant development, and we believe that it should be intelligible to any student or other potential user who has completed an introductory university course in biology or botany. Without preparing a text on plant anatomy, we have tried to provide enough fundamental information upon which to base an account of developmental phenomena. At the same time, in expanding each topic, we have tried to put the reader in contact with current prob-



Desfass		
Preface	•	 XIII

lems and interpretations so that direct progression to the literature is possible.

Although we assume full responsibility for the contents of this book, the influence of many others has played an important part in its development. We shall always be indebted to the two distinguished botanists to whom this second edition, like the first, is dedicated. Their pioneering investigations in experimental morphogenesis, and the vision of this field that they expounded, inspired and influenced a generation of developmental botanists, particularly those of us who were fortunate enough to be their students. Many colleagues and students have also contributed to this work in numerous discussions and debates on the problems of development. We are particularly grateful to our students whose penetrating questions, unencumbered by preconceived notions, have so often provided a stimulus to clearer thinking. Finally, we hope that the result of our efforts will justify the confidence of the many colleagues who have urged us to undertake this revision.



Acknowledgments

We are most appreciative of those who contributed in particular ways to the preparation of this volume. Mrs. S. F. Rowley skillfully produced the manuscript from our nearly illegible script and patiently accommodated numerous editorial revisions. Ms. Sharon Pulvermacher and Ms. Colleen Shepstone are to be complimented for their fine artistic work, as are Mr. Dennis Dyck and Ms. P. J. Rennie for many of the included photographs. Finally we are indebted to Dr. Margaret Steeves for advice and assistance on many occasions, and especially for the preparation of the index.