An Introduction to Plant Structure and Development

Plant Anatomy for the Twenty-First Century
Second Edition

This is a plant anatomy textbook unlike any other on the market today. As suggested by the subtitle, it is plant anatomy for the twenty-first century. Whereas traditional plant anatomy texts include primarily descriptive aspects of structure with some emphasis on patterns of development, this book not only provides a comprehensive coverage of plant structure, but also introduces, in some detail, aspects of the mechanisms of development, especially the genetic and hormonal controls, and the roles of the cytoskeleton. The evolution of plant structure and the relationship between structure and function are also discussed throughout the book. Consequently, it provides students and, perhaps, some teachers as well, with an introduction to many of the exciting, contemporary areas at the forefront of research, especially those areas concerning development of plant structure. Those who wish to delve more deeply into areas of plant development will find the extensive bibliographies at the end of each chapter indispensible. If this book stimulates a few students to become leaders in teaching and research in plant anatomy of the future, the goal of the author will have been accomplished.

CHARLES B. BECK, Professor Emeritus of Botany at the University of Michigan, received his PhD degree from Cornell University where he developed an intense interest in the structure of fossil and living plants under the influence of Professor Harlan Banks and Professor Arthur Eames. Following post-doctoral study with Professor John Walton at Glasgow University in Scotland, he joined the faculty of the University of Michigan. At Michigan he served one term each as Chairman of the Department of Botany and Director of the Museum of Paleontology. His graduate students pursued research in either plant structure and development or paleobotany. He taught courses in plant anatomy, plant morphology and paleobotany over a period of 35 years.

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Charles B. Beck
University of Michigan

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To
My wife, Janice,
and our daughters, Ann and Sara
for their love, encouragement,
and enduring support,

and

to my students,

David Benzing
Robert Chau
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Margaret Knaus
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who are a continuing inspiration and
from whom I have learned much.

It is important that students bring
a certain ragamuffin barefoot
irreverence to their studies; they
are not here to worship what is
known but to question it.

Jacob Bronowski
The Ascent of Man (1975)

Contents

Preface to the second edition

Although it has been only five years since this book was first published, research activity during this period in many areas of plant development has resulted in much new and important information. The basic information on plant structure is quite stable. As a result, inclusion of new information about various aspects of development comprise the major changes in this 2nd edition. In addition, a new section on the evolution of tracheary elements has been added.

The areas expanded and/or upgraded include the structure and function of the cytoskeleton, and its roles in cell wall formation and pollen tube tip growth; the role of auxin and other hormones in development, especially in the development of tracheary elements, as well as in cambial activity and tissue patterning, and the role of PIN proteins in the movement of auxin from cell to cell by auxin efflux transporters. The discussion on the mechanism of movement of stomatal guard cells has been expanded and improved. Sections on long-distance transport in the secondary xylem and phloem have been modified to emphasize widely accepted mechanisms of transport, and the discussion of bidirectional transport in the phloem has been expanded. The discussion of gravitropism has been brought up to date. Finally, throughout the book, discussions of the role of genetics in plant development have been expanded.

I believe the changes listed above have made the book more useful to advanced students and researchers without adversely affecting its usefulness as an introductory plant anatomy textbook. It is not designed to be used as the only source of information in a course in plant anatomy, i.e., to take the place of the teacher, but rather, to be a supplement to the teacher's lectures and a means for the student to reinforce information from the teacher and the laboratory exercises. The book can, of course, also be an original source of information for students beyond that provided by the teacher. When used in a course that emphasizes development, the student will have the opportunity to expand his or her knowledge of plant structure, and in a course that emphasizes plant structure, the student can expand his or her knowledge of plant development. Ideally, however, a twenty-first century course in plant anatomy should consist of an integration of structure and development. It is this ideal that I have tried to promote in the design and preparation of this book.

For granting me permission to use photographs in this 2nd edition of the book, I express my appreciation to university and commercial publishers and all other copyright holders. I am especially grateful to Professor Philip Gingerich for allowing me to use the facilities and services of the University of Michigan Museum of Paleontology, and to three very talented persons in this unit, Bonnie Miljour, senior scientific

illustrator, Cindy Stauch, business administrator, and Christina Minor, research secretary who were so helpful in many ways.

I express my gratitude to Dominic Lewis, commissioning editor, life sciences, Rachel Eley, assistant editor, life sciences, Caroline Brown, production editor, and Lesley Bennun, copy-editor, and acknowledge their important roles in the preparation and production of this book.

Finally, I owe a special debt of gratitude to my wife, Janice, whose patience and encouragement have contributed so importantly to the completion of this project.

Charles B. Beck
Ann Arbor, 2009

Preface

Since my introduction to plant anatomy by William Strickland at the University of Richmond and my interaction with Arthur Eames and Harlan Banks at Cornell University during graduate study, I have been entranced by the elegant beauty of plant structure. At the University of Michigan I taught both paleobotany and plant anatomy for many years, and served as committee chair for graduate students, some of whom studied fossil plants and others of whom worked on the structure and development of extant taxa. During the past several decades during which the introduction of new techniques of study at the subcellular and molecular levels has resulted in a resurgence of research throughout the world, my interest in the development of plant structure has grown steadily.

Many books on plant structure, some highly technical, have appeared since the publication of the seminal textbooks of Katherine Esau during the 1950s and 1960s, but no single book that, in my opinion, incorporates both the basic knowledge of plant anatomy and contemporary information and ideas about the development of structure and form that could be used as an effective introductory textbook. Consequently, I have tried to meet the challenge of preparing such a book. In each chapter I have presented what I consider to be the fundamental knowledge essential for an understanding of basic plant structure and development and have integrated with this the results of some of the most significant recent research on plant development. Whereas emphasis throughout the book is on structure and development, I have also included sections on evolution and function where it seemed essential and appropriate to do so. The application of cellular and molecular biological approaches and techniques in the study of plant development has revolutionized the field. Understanding of the integrative significance of plasmodesmata and the concept of the symplast have led to an appreciation and widespread acceptance of the organismal theory of plant multicellularity which in turn has influenced research on plant development. Exciting and significant areas of research such as the role of the cytoskeleton in development, signal transduction, genetic control of development, among others have greatly advanced our understanding. I have not treated the very important subject of the genetic control of development in any depth because it requires a much deeper knowledge of genetics than the undergraduate for which this book is written is likely to have attained. I have, however, included references to important genetic studies in the bibliographies of several chapters. Other subjects may not be as fully covered as some teachers and researchers would desire, but they are very likely to find pertinent references to literature on those subjects in the extensive bibliographies to which they can direct their students who have the necessary backgrounds.

Diverging from the approach in many textbooks, I have included in this book tentative conclusions that are essentially still hypotheses, and discussions of research that is controversial, often providing opposing viewpoints. I believe that, in addition to providing well-established information on a subject, a textbook should also provide the student with an understanding of the nature of ongoing scientific research.

In order to make this book more readable for the undergraduate, I have omitted most literature citations in sections of the text in which the basic, widely accepted knowledge in the field is presented, but have included some references of historical importance in the references at the end of each chapter. On the other hand, when presenting new information, ideas, and conclusions that are not yet widely accepted, I have cited in the text and included in the references the sources of this information. Thus, students as well as researchers who wish to consult the original papers may find the reference sections useful.

My objective has been to prepare a new plant anatomy textbook for a new century, incorporating the best research in the most active and significant areas with the widely accepted common knowledge that provides the foundation of the field. Only you the readers can decide whether or not I have succeeded.

Charles B. Beck
Ann Arbor, 2004

Acknowledgements

One's knowledge comes from many sources. Not least are the research and writings of many predecessors in the field. Men and women such as Nägeli, De Bary, Strasburger, Haberlandt, Van Tieghem, Solereder, Jeffrey, Eames, Bailey, Metcalfe and Chalk, Esau and countless others have provided the foundation upon which current-day researchers are building. To these, whom sometimes we forget, we owe a debt of gratitude. I acknowledge a profound debt to my college and university teachers, William Strickland and Robert Smart who introduced me to plant structure in the first place, Arthur Eames and Harlan Banks who widened my horizons and reinforced my understanding of the fundamentals of plant anatomy, and to John Walton who encouraged me to take risks and taught me how to write. I acknowledge, as well, the significant contributions to my knowledge of the many researchers who are currently active in the field.

Direct assistance during the preparation of this book has come from many sources. I feel particularly indebted to colleagues who have critically read chapters in manuscript and made important suggestions for change and improvement. These are Professor William Stein of the State University of New York, Binghamton who read several chapters, Professor Shirley Tucker of the University of California at Santa Barbara, Professor Nancy Dengler of the University of Toronto, and Professor Darleen DeMason of the University of California, Riverside. Other colleagues have provided information on special topics. Professor Peter Ray of Stanford University provided information on the functional significance of the optical qualities of epidermal cells in leaves, Professor Judy Jernstedt of the University of California at Davis provided information on contractile roots, Professor Larry Nooden of the University of Michigan was a source of important information on several aspects of plant physiology, Professor Robert Fogel of the University of Michigan provided information on mycorrhizae, and Professor Edward Voss and Dr. Christiane Anderson of the University of Michigan were valuable sources of information on plant taxonomy. To all of these I express my sincere appreciation.

Professor Philip Gingerich, Director of the Museum of Paleontology at the University of Michigan, made available to me the resources and services of the Museum. Preparation of this book would not have been possible without this assistance, and to Phil I express my sincere gratitude. The illustrations are nearly as important as the text in a plant anatomy book. In this book all original line drawings were finished by Bonnie Miljour, artist *par excellence* of the Museum of Paleontology. Ms. Miljour also grouped and placed all illustrations in electronic files. The importance to this project of her great expertise cannot be overemphasized. Thank you, Bonnie, for the beauty of your work and for your very important contribution to this book. Two members of the Museums

office staff, Cindy Stauch and Meegan Novara, were also of inestimable assistance in many ways. I express my sincere appreciation to them.

The original photographs were taken primarily by two University of Michigan photographers, Louis Martonyi, now deceased, who was photographer for the Department of Biology during the 1980s, and David Bay, current photographer for the Department of Ecology and Evolutionary Biology. Thank you, David, for your excellent work. A few photographs were taken by the author in the facilities of the Microscopy and Image-analysis Laboratory of the University of Michigan Medical School. This was made possible by the kindness of the Laboratory Manager, Chris Edwards and with the technical assistance of Shelley Almburg, to both of whom I express my appreciation. I express my sincere gratitude to colleagues who provided photographs: Professor Pedro J. Casero of Universidad de Extremadura, Badajoz, Spain; Professor P. Dayanandan of Madras Christian College, India; Dr. Elisabeth de Faÿ of Université Henri Poincaré, Nancy, France; Professor Nancy Dengler of the University of Toronto, Canada; Dr. Katrin Ehlers of the Justus-Liebig-Universität, Giessen, Germany; Dr. Irene Lichtscheidl of Universität Wien, Austria; Dr. E. Panteris of the University of Athens, Greece; and Dr. Koichi Uehara of Chiba University, Japan. Professor P. Maheshwari of the University of New Delhi sent me many excellent slides during his lifetime, many of which have been photographed for use in this book. I have also used many illustrations from published sources, and I express my gratitude to the individuals, commercial publishers, university presses, and professional societies that have granted permission for the use of their copyrighted materials.

Although every effort has been made to secure necessary permissions to reproduce copyrighted material in this work, it has proved impossible in two cases to trace the copyright holders. The copyright holder of the original illustration from Lehninger (1961), which I have used as my Fig. 3.7a, is Dr. A. E. Vatter. The copyright holder of the original illustrations from Eames and MacDaniels (1925), which I have used as my Figs 13.3, 13.4, 14.5, 16.15c, and 16.21 is David Eames. Appropriate acknowledgements will be included in any reprinting or in any subsequent edition of this book if the copyright holders are located.

In order to understand copyright law, which varies somewhat throughout the world, I called on my friend, Professor John Reed of the University of Michigan Law School, for advice. He directed me to Professor Molley Van Houweling, a specialist in copyright law, who gave me valuable information. I am grateful to these colleagues.

Without the resources of the University of Michigan Library this book could not have been written, and the excellent assistance of the reference librarians in the Shapiro Science Library is acknowledged with gratitude.

To the editors of Cambridge University Press I express my gratitude, and acknowledge their important roles in the preparation and production of this book. In particular, I wish to thank Ward Cooper, commissioning editor, life sciences; Clare Georgy, assistant editor, life

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Finally, I must acknowledge friends and family who through their interest and support have made a contribution to this project greater than they can imagine. Every morning for many years past and during the several years of this project I have joined friends for coffee. We call the group the Coffee Klatch. Members have included Robert Lowry, cytogeneticist and microscopist, Erich Steiner, plant geneticist, Norman Kemp, animal morphologist, Ralph Loomis, teacher of English literature, Harry Douthit, microbiologist, James Cather, developmental biologist, Michael Wynne, phycologist, Barbara Brown, university bus driver, and me. Conversation has ranged over a broad spectrum of interests and activities, but almost never on "the book." Interaction with this wonderful group of university colleagues has provided me with a daily means of relaxation and a time to forget about cells, tissues, microtubules, and actin microfilaments. On the other hand, I have felt the subtle but genuine support for me and this project by members of the group. So I express my sincere appreciation to my friends of the Coffee Klatch.

One person, however, stands out above all others in importance. My wife, Janice, has supported me with remarkable patience and understanding during work on this book. She has added to her busy schedule many activities for which I would ordinarily have taken responsibility and has been a constant source of support and encouragement. Thank you, Sweetheart, for being the wonderful person you are, and for your most important contributions to this project.

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