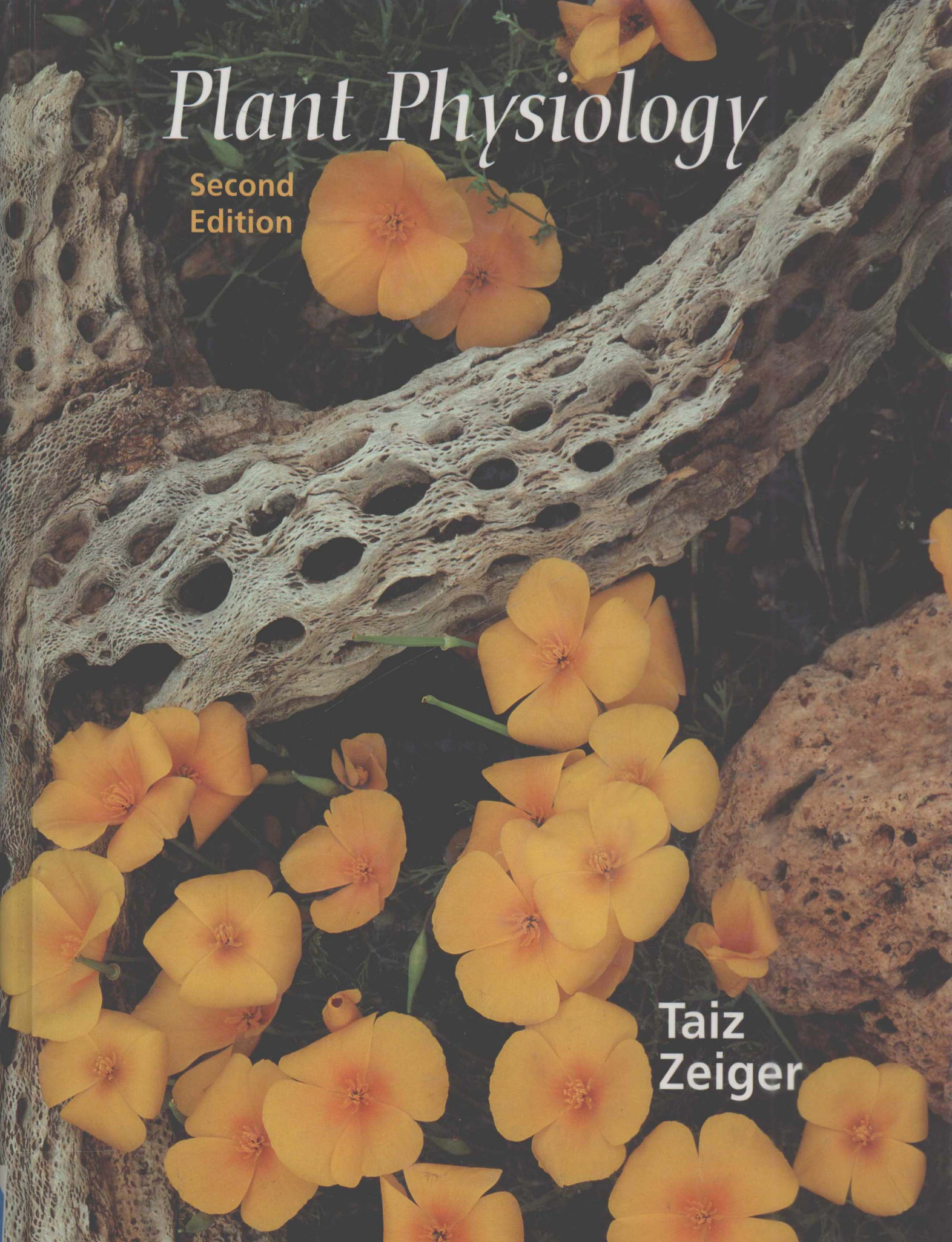
Plant Physiology

Second Edition



Taiz
Zeiger

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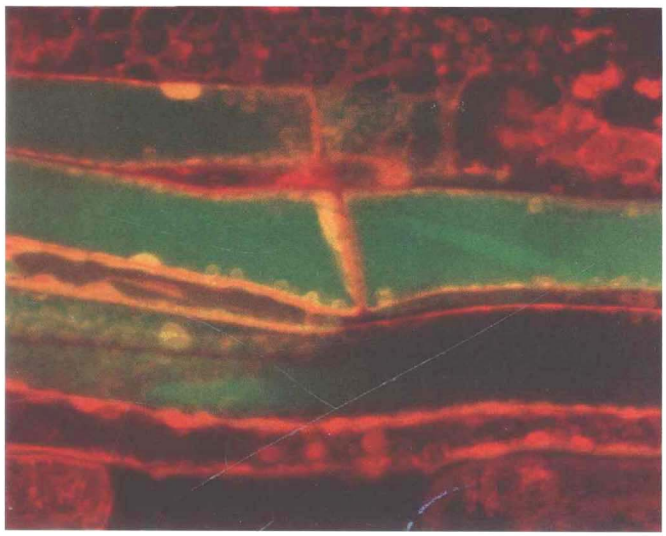

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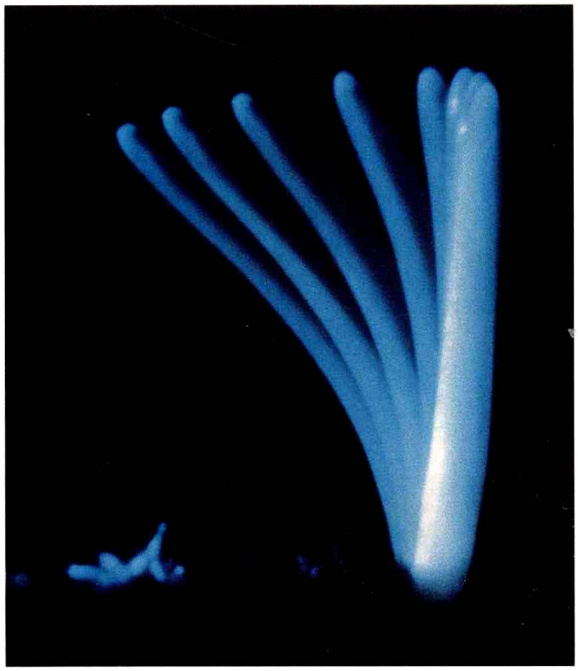

PLANT PHYSIOLOGY, *Second Edition*

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FRONT COVER
Mexican goldpoppies blooming beside the vascular skeleton of a cholla cactus (*Opuntia* sp.).

BACK COVER
Close-up of the spines and flower of a strawberry hedgehog cactus. Front and back cover photographs by Willard Clay.

THE HALF-TITLE PAGE
Localization of the sucrose–H^+ symporter in the phloem. This micrograph shows a single companion cell from broad-leaved plantain (*Plantago major*) stained with two fluorescent dyes. One of the dyes (green) is (indirectly) linked to an antibody that is specific for the PmSUC2 sucrose–H^+ symporter. The second dye (blue) binds to DNA. Since the two dyes are found on a single phloem cell, which is always adjacent to a sieve element, the sucrose symporter is concluded to be located in the companion cell membrane in this species. (From Stadler et al. 1995, courtesy of N. Sauer. See page 266 in Chapter 10.)

THE FRONTISPIECE
TOP: Tip-growing pollen tubes exhibit a steep intracellular gradient of calcium ion concentration, with the highest levels at the growing tip. Pollen tubes from three species of plants were microinjected with a fluorescent calcium indicator dye to demonstrate this Ca^{2+} gradient, ranging from about 1 μM at the extreme tip to about 0.2 μM at the base. (Photo from Hepler 1997, courtesy of P. Hepler. See page 436 in Chapter 15.)

BOTTOM: The nucleation and propagation of ice in the stem, buds, and leaves of rhododendron (*Rhododendron* sp.). Emission of heat (colored blue and rust) during ice formation was detected by infrared thermography. Ice nucleation was observed to begin in the stem (lower right-hand corner), and then to spread to buds and leaves (blue and rust-colored areas). Even though a drop of a suspension of the ice-nucleating bacteria *Pseudomonas syringae* (yellow spot on the center leaf of the right-hand side) froze, initial nucleation and freezing started in the stem. (From Wisniewski et al. 1997, courtesy of M. Wisniewski, © American Society of Plant Physiologists, reprinted with permission. See page 740 in Chapter 25.)

THE TITLE PAGE
Phloem tissue of a bean doubly stained with a locally applied dye (red) and a translocated dye (green). Protein deposited against the plasma membrane and the sieve plate does not impede translocation. A crystalline P protein body is stained by the green dye. Phloem plastids are evenly distributed around the periphery of the cell. (From Knoblauch and van Bel 1998, courtesy of A. van Bel. See page 275 in Chapter 10.)

THIS PAGE
Time-lapse photograph of a corn coleoptile growing toward unilateral blue light. Unilateral blue light was given from the left. The consecutive exposures were made 30 minutes apart. Note the increasing angle of curvature as the coleoptile bends. (Photograph courtesy of M. A. Quiñones. See page 519 in Chapter 18.)

Preface

IT IS A PRIVILEGE TO PRESENT TO OUR READERS the second edition of *Plant Physiology*, which follows the first edition by seven years. The challenge of condensing, organizing, and synthesizing all the available knowledge in the field was daunting enough at the time of the first edition; the explosion of progress since 1991 makes these tasks even more demanding for the second edition.

The strength of the second edition, like that of the first, lies primarily with the outstanding group of scientists who have contributed their expertise and historical perspectives to this complex effort. They deserve all the credit for selecting the information that best represents the true conceptual advances in the field of plant physiology. Our task has been to ensure that all the topics were adequately covered and that the various topics were presented in a uniform style and level of difficulty. The editorial division of labor was as follows: E.Z. was responsible for Chapters 3, 4, 5, 7, 8, 9, 12, 18, and 25; L.T. was responsible for Chapters 1, 2, 6, 13, 14, 15, 16, 17, 19, 20, 21, 22, 23, and 24; Chapters 10, 11, and 25 have been edited by both of us. Several of the chapter authors from the first edition did not join us for this second edition, but their important contributions are still central to many of the chapters in the book. We wish to thank them for their previous efforts on behalf of the book: George W. Bates, Donald P. Briskin, Anthony L. Fink, Shimon Gepstein, Adrienne R. Hardham, Frank Harold, George H. Lorimer, John W. Radin, Stanley J. Roux, Thomas David Sharkey, Richard G. Stout, Daphne Vince-Prue, and Stephen M. Wolniak.

As in the first edition, much of the credit for integration and pedagogical style belongs to our developmental editor, James Funston. We feel fortunate to have engaged such a wise, creative, and endlessly patient advisor for both the first and second editions of *Plant Physiology*. A major improvement in the preparation of the second edition has been the convenience of using email and the internet, which

enabled us to track down information much more efficiently than before, often from the comfort of our own home offices. The availability of email enabled us to rapidly check the accuracy of information with scientists spread all over the globe. Email also helped us to make pedagogical decisions, since we were able to contact large numbers of people to determine their preferences. Thus the number of colleagues around the world who have provided critical input into the preparation of this book is truly unprecedented.

Perhaps the most important innovation of the second edition is the new publisher, Sinauer Associates. We wish to extend our gratitude to Andy Sinauer for his initial faith in the book and for his continued encouragement during the ensuing months of its preparation; to our editor Nan Sinauer for her infinite patience, adroit decision making, and tireless shepherding of the manuscripts from first drafts to final copy; and to Suzette Stephens, Stephanie Hiebert, Chris Small, Janice Holabird, and Jefferson Johnson for their significant contributions.

Last but not least, we wish to thank our departmental colleagues, postdoctoral fellows, and students for their precious help and for enduring the extended periods of "total immersion" that were often required to get the job done. Finally, L.T. wishes to thank his wife, Lee Taiz, whose faith in the project sometimes exceeded his own, and whose love and support sustained him whenever the road became bumpy.

Lincoln Taiz

Eduardo Zeiger

July 1998

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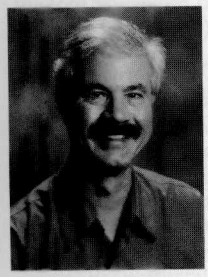
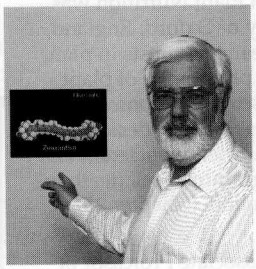


Lincoln Taiz is a Professor of Biology at the University of California at Santa Cruz. He received his Ph.D. in Botany from the University of California at Berkeley in 1971. Dr. Taiz's current research interests include the structure and regulation of vacuolar H^+-ATPases, mechanisms of heavy metal tolerance, and the roles of aminopeptidases in plant development.



Eduardo Zeiger is a Professor of Biology at the University of California at Los Angeles. He received a Ph.D. in Plant Genetics at the University of California at Davis in 1970. His research interests include stomatal function, the sensory transduction of blue light responses, and the study of stomatal acclimations associated with increases in crop yields.

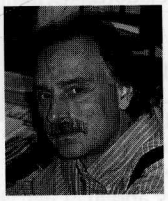
Principal Contributors

Richard Amasino is a Professor in the Department of Biochemistry at the University of Wisconsin–Madison. He received a Ph.D. in Biology from Indiana University in 1982 in the laboratory of Carlos Miller, where his interests in the induction of flowering were kindled. One of his research interests continues to be the mechanisms by which plants regulate the timing of flower initiation. (Chapter 24)

Paul Bernasconi is Director of Biochemistry at Novartis Crop Protection, Inc., in Research Triangle Park. His Ph.D. in Plant Biology and Protein Biochemistry was earned in 1987 at Lausanne University in Switzerland. His present work is focused on the biochemistry of herbicide, insecticide, and fungicide targets for crop protection. (Chapter 19)

Robert E. Blankenship is a Professor of Chemistry and Biochemistry at Arizona State University in Tempe. He received his Ph.D. in Chemistry from the University of California at Berkeley in 1975. His professional interests include mechanisms of energy and electron transfer in photosynthetic organisms, and the origin and early evolution of photosynthesis. (Chapter 7)

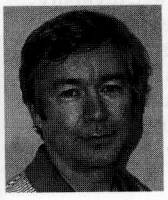
Arnold J. Bloom is a Professor in the Department of Vegetable Crops at the University of California at Davis. He received a Ph.D. in Biological Sciences at Stanford University in 1979. His research focuses on plant-nitrogen relationships, especially the differences in plant responses to ammonium and nitrate as nitrogen sources. (Chapters 5 and 12)



Ray A. Bressan is Professor of Plant Physiology at Purdue University. He received a Ph.D. in Plant Physiology from Colorado State University in 1976. Dr. Bressan has studied the basis of salinity and drought tolerance for several years. His recent interests have also turned toward the way plants defend themselves against insects and fungal disease. (Chapter 25)

John A. Browse is a Professor in the Institute of Biological Chemistry at Washington State University. He received his Ph.D. from the University of Aukland, New Zealand, in 1997. Dr. Browse's research interests include the biochemistry of lipid metabolism and the responses of plants to low temperatures. (Chapter 11)

Bob B. Buchanan is Professor of Plant and Microbial Biology at the University of California at Berkeley. After working on photosynthesis, Dr. Buchanan turned his attention to seed germination, where his findings have led to technologies that are currently under precommercial development. (Chapter 8)

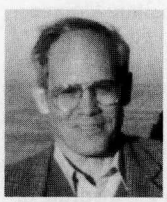


Daniel J. Cosgrove is a Professor of Biology at the Pennsylvania State University at University Park. His Ph.D. in Biological Sciences was earned at Stanford University. Dr. Cosgrove's research interest is focused on plant growth, specifically the biochemical and molecular mechanisms governing cell enlargement and cell wall expansion. His research team discovered the cell wall loosening proteins called expansins and is currently studying the structure, function, and evolution of this gene family. (Chapters 3, 4, and 15)

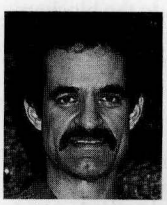
Peter J. Davies is a Professor of Plant Physiology at Cornell University. He received his Ph.D. in Plant Physiology from the University of Reading in England. His present interests are using genotypes and polygene analysis to elucidate the role of hormones in potato tuberization, stem elongation, and plant senescence. He is the compiler and editor of the principal monograph on plant hormones and has also worked on the isolation of genes of gibberellin biosynthesis. (Chapter 20)

Malcolm C. Drew is Professor of Plant Physiology and Plant Biotechnology at Texas A & M University. His Ph.D. in Plant Nutrition was earned at the University of Oxford, England, in 1966. Dr. Drew's research interests in plant physiology include the physiology of plant roots and plant responses to environmental stress, particularly excess salinity, desiccation, oxygen shortage, and nutrient deficiency. His current work is on programmed cell death in roots and phytoremediation. (Chapter 25)

Susan Dunford is an Associate Professor of Biological Sciences at the University of Cincinnati. She received her Ph.D. from the University of Dayton in 1973 with a specialization in plant and cell physiology. Dr. Dunford's research interests include long-distance transport systems in plants, especially translocation in the phloem, and plant water relations. (Chapter 10)



Donald E. Fosket is Professor of Developmental and Cell Biology at the University of California at Irvine. He received his Ph.D. in Biology from the University of Idaho and subsequently did postdoctoral work at Brookhaven National Laboratory and at Harvard. Currently he is investigating the molecular mechanism controlling plant cell polarity at the Salk Institute in La Jolla, California. (Chapters 16, 21, and 24)



Jonathan Gershenzon is a Director of the newly established Max Planck Institute for Chemical Ecology, Jena, Germany. He received his Ph.D. from the University of Texas at Austin in 1984 and did postdoctoral work at Washington State University. His research focuses on the biosynthesis of plant secondary metabolites, and in establishing the roles of these compounds in plant–herbivore interactions. (Chapter 13)

Paul M. Hasegawa is Professor of Plant Physiology at Purdue University. He earned a Ph.D. in Plant Physiology at the University of California at Riverside. His research has focused on plant morphogenesis and the genetic transformation of plants. He has used his expertise in these areas to study many aspects of stress tolerance in plants, especially ion homeostasis. (Chapter 25)

Joseph Kieber is an Assistant Professor in the Department of Biological Sciences at the University of Illinois at Chicago. He earned his Ph.D. in Biology from the Massachusetts Institute of Technology in 1990. Dr. Kieber's research interests include the role of hormones in plant development, with a focus on the signaling pathways for ethylene and ctyokinin, as well as circuitry regulating ethylene biosynthesis. (Chapter 22)

Ronald J. Poole is a Professor of Biology at McGill University, Montreal. He received his Ph.D. from the University of Birmingham, England, in 1960. Dr. Poole's research interests are in ion transport in plant cells, including electrophysiology, biochemistry, and molecular biology of ion pumps and channels. (Chapter 6)

James N. Siedow is a Professor in the Department of Botany at Duke University. He earned his Ph.D. in Botany at Indiana University in 1972. Professor Siedow's long-term research interests have involved the study of redox reactions in biological systems, with a focus on the pathways of plant respiration. Included among these studies have been the characterization of the cyanide-resistant respiratory pathway and its regulation in plants. (Chapter 11)

Wendy K. Silk is Professor and Plant Scientist at the University of California at Davis. She received her Ph.D. from the University of California at Berkeley. Dr. Silk uses approaches from mathematics and physics to analyze the physiology of growth and plant responses to environmental variation. Research interests include morphogenesis, biomechanics, and stress physiology. (Chapter 16)

Jane Silverthorne is an Associate Professor in the Department of Biology at the University of California at Santa Cruz. She received her Ph.D. in Biology from the University of Warwick in the United Kingdom in 1980. Her research interests focus on the role of phytochrome in the regulation of molecular aspects of plant development. (Chapter 17)

Thomas C. Vogelmann is a Professor of Plant Physiology at the University of Wyoming. He received his Ph.D. from Syracuse University in 1980, specializing in plant development, and he subsequently did postdoctoral work in plant photobiology at the University of Lund, Sweden. His current research is focused on how plants interact with light. Specific research areas include plant tissue optics, leaf structure function related to photosynthesis and environmental stress, and plant adaptations to the environment. (Chapter 9)

Ricardo A. Wolosiuk is Professor in the Instituto de Investigaciones Bioquímicas at the University of Buenos Aires. He received his Ph.D. in Chemistry from the same university in 1974. Dr. Wolosiuk's research interests concern the modulation of chloroplast metabolism and the structure and function of plant proteins. (Chapter 8)

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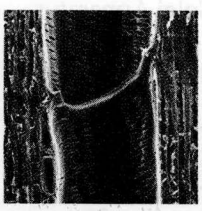
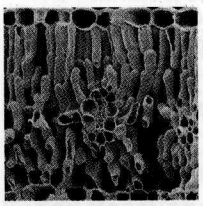
Table of Contents



UNIT I

Transport and Translocation of Water and Solutes 59



UNIT II

Biochemistry and Metabolism 153

8 *Photosynthesis: Carbon Reactions 195*

UNIT III
Growth and Development 377