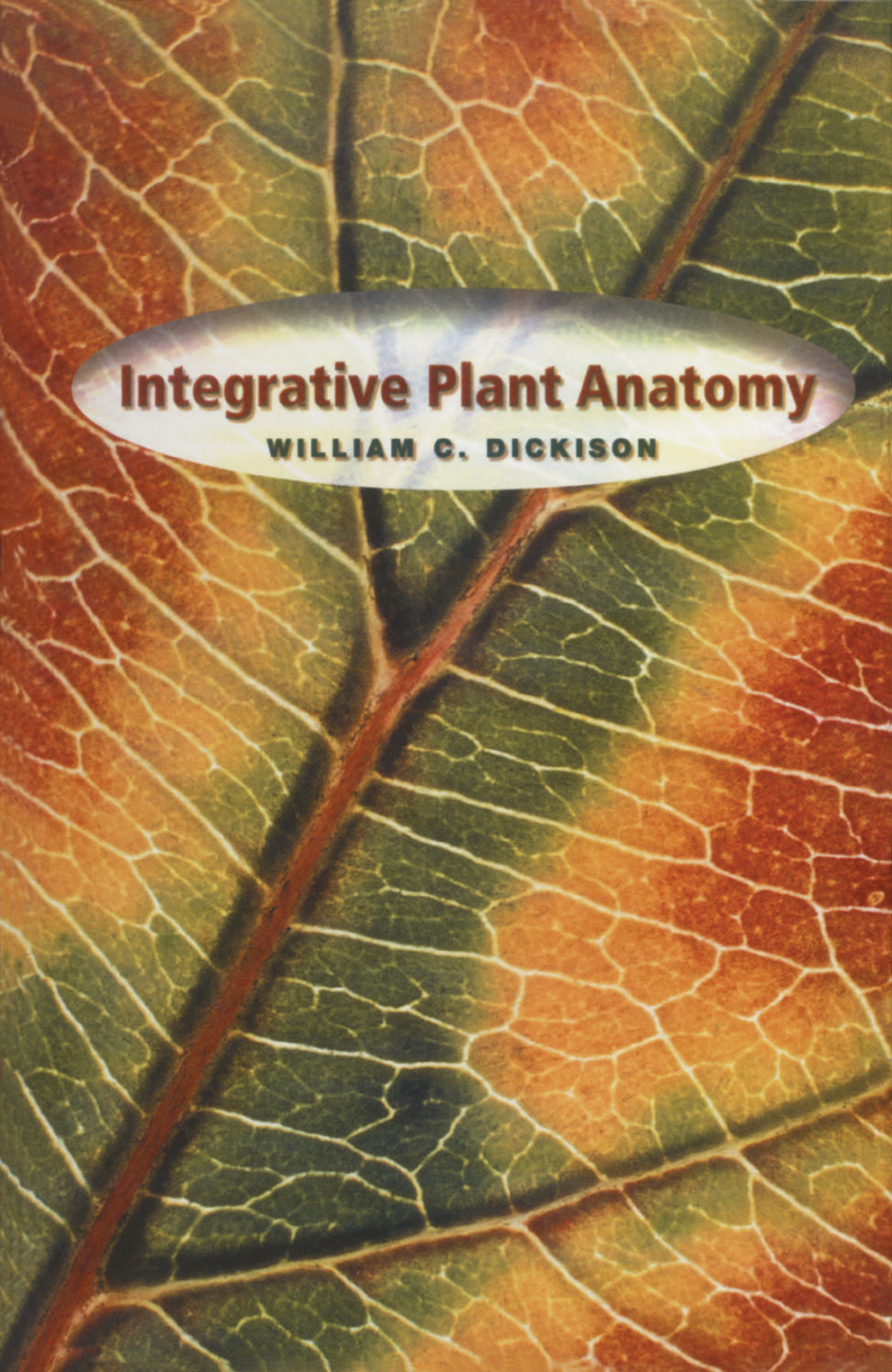
Integrative Plant Anatomy
WILLIAM C. DICKISON

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Integrative Plant Anatomy

WILLIAM C. DICKISON

San Diego San Francisco New York Boston
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As I was writing the final chapter of this book, I realized that I was living the final chapter of my life. It is with this thought that I dedicate this book to my grandchildren

Andrew Campbell
Erica Grace
William Campbell

in remembrance of their grandfather.

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PREFACE

During the course of my career as a structural botanist, I have occasionally been asked: What value is plant anatomy and how does it relate to other fields of study? *Integrative Plant Anatomy* was written in response to such questions and to present the subject of plant anatomy as a multifaceted, interdisciplinary, and relevant field of inquiry. Plant anatomy, or the developmental and comparative study of plant cells, tissues, and organs, is a botanical discipline with a long tradition. Many individuals have emphasized the fact that anatomy is both a descriptive and an experimental science. In other words, anatomists employ critical and extensive observation, resulting in the compilation, codification, and analysis of descriptive data, but they also use the analytical methods of the experimental sciences. Each methodology has different advantages and limitations, and each requires distinct skills on the part of the investigator. Much anatomical research and most practical courses in plant anatomy historically have included topics centered on the systematic, phylogenetic, developmental, and functional aspects of the subject. Although there are now many outstanding textbooks and comprehensive reference works that emphasize one or more of these approaches, inadequate attention has been given to the overall relationship of anatomy to other areas of botany, as well as to the nonbiological sciences, the arts, and numerous other fields of human endeavor. Clearly, a solid foundation in basic plant anatomy is required in order for individuals to fully participate in the diversity of modern interdisciplinary studies. The intent of this book is to bridge these gaps by consolidating widely scattered information into a series of chapters that highlight the principal contributions of plant anatomy to the solution of a number of current and future problems. The selection and detail of the topics is meant to provide a balanced and informative synthesis both for students of botany and for people without any special

knowledge of plants but who might want to become acquainted with this interesting branch of plant biology. Most books treat the subject of plant anatomy in basically the same way, discussing cells, tissues, tissue systems, and organs in sequence. I attempt to present the discipline of plant anatomy in a different light and show how structural botany is integrated with other modern fields. At the very least, I hope that this volume will result in a renewed awareness of the many interrelated applications of this classical subject and why individuals conversant with the details of structural botany are necessary and useful.

The first four chapters provide an overview of higher plant organization and structure. This can serve as the basis for further study of the subject, or provide students of botany with an introduction to the field. Later chapters discuss these anatomical concepts and approaches at greater length in relation to more specialized topics. This book centers on seed plants, especially angiosperms. It presents the basic concepts and terminology of the study of plant anatomy, but it also emphasizes applied and economic aspects of the discipline. Examples or case histories are provided in which a knowledge of plant structure has been or could be an important tool in resolving a problem or contributing to our general understanding of some other discipline. Because the literature is voluminous, the additional readings at the end of each chapter include a sampling of recent references as well as classical citations.

In 1992, the late Professor Dr. Klaus Napp-Zinn of the University of Cologne and I agreed to collaborate on a book whose central theme would be the integration of plant anatomy with other fields. Professor Napp-Zinn died unexpectedly during the early stages of our collaboration. This volume represents the book that we had in mind, although its content reflects entirely my own judgment and work. I wish to thank my departed friend not only for his numerous contributions to the field of plant anatomy but also for his enthusiasm for this project.

William C. Dickison
November, 1999

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Finally, and most of all, I acknowledge my wife, Marlene, for her constant love, unfailing encouragement, and sustaining interest in the progress of this book.

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1

ANATOMICAL FOUNDATION OF THE PLANT BODY: AN OVERVIEW

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1 PLANT GROWTH, DEVELOPMENT, AND CELLULAR ORGANIZATION

Despite enormous differences in plant size, all higher plant bodies consist of a central axis divided into two regions, the mostly above ground **shoot** and the below ground **root.** The shoot is further differentiated into the lateral photosynthetic appendages, the **leaves,** and the axial component on which the leaves are attached, the **stem.** Reproductive organs, sporangia and/or sporophylls, form at reproductive maturity. Each organ in turn is composed of **tissues,** collections of one or more cell types that share a common physiological and structural function and often a common origin. As the shoot grows, it forms new increments of stem and new leaves in an acropetal direction, that is, from the base of the plant upward.

PLANT GROWTH

Growth is a genetically programmed developmental process involving cell division, selective cell enlargement, and maturation. Roots, like shoots, also become extended apically, increasing in length. This manner of growth is traceable to a small region of cells at the tip of the stem and the root that is characterized by the formation of new, and eventually more differentiated cells, by repeated subdivision and cell expansion. These regions of potentially unlimited growth and active cell division are termed **meristems.** They represent a defining feature of plants. All growth and organ formation of the plant is initiated and largely controlled by the meristems and their subordinate regions.

The concept of meristem refers to the collection of actively dividing cells, termed **initials,** plus their most recent **derivatives.** Functionally, vegetative meristems are **indeterminate,** that is, not limited in their capacity to continue

the development of the axis. The actual elongation of the axis occurs by means of cellular enlargement, a process that can result in a 10- to 1000-fold increase in cell volume and that is associated with an increase in internal turgor pressure and irreversible changes in the cell wall. Vascular plants are characterized by a so-called open growth pattern in which new cells, tissues, and organs are regularly initiated throughout the plant's life. This type of growth relies upon the existence of small aggregations of cells that occur at specific sites in the plant body, retaining their genetic potential of active cell division.

In addition to initiating new tissues and organs and controlling the pattern of cell and tissue differentiation, meristems communicate signals to and from the remainder of the plant body, while at the same time maintaining themselves as organized, formative regions. It has long been assumed that variations in the behavior of meristems, that is, the frequency and orientation of division planes, are major factors in determining the shape of plant organs. Recent studies, however, have challenged a number of long-standing assumptions about the significance and function of cell division in organ formation and the role of localized meristems in morphogenesis. Nevertheless, there is agreement that the remarkably complex process of overall plant growth is dependent upon the presence of permanently "embryonic" meristematic tissue.

Meristem Function

It is possible to identify meristems by their topographic positions and by their capacity for cell division. Meristems restricted to the extreme tips of stems, branches, and roots are called **apical meristems** and their activity results in **primary growth** and an associated increase in axis length. The concept of the **promeristem** has been utilized to refer to the core of centrally positioned initial cells and their immediate derivatives that have yet to show visible evidence of differentiation and a progression to a more specialized form or function. The tissues that arise directly from these apically located regions are called **primary tissues.** They contribute to growth in length as well as to limited growth in the width of organs. The growing tip of the shoot consists of a pool of meristematic cells whose derivatives result not only in organ length but also in the formation of regularly spaced, undifferentiated subapical mounds of cells on the flanks of the apical dome. These cell groups are called **primordia.** They develop into new leaves, branches, or floral parts in regular sequence following a course of development that is species specific. The apical meristem of roots, on the other hand, is subapical and not only contributes derivatives to the root tissue that account for an increase in root length but also produces cells distally to form the outer root cap. The exact boundary, however, between the core of actively dividing cells and the proliferative subapical zone is often difficult to clearly demarcate.

The differential expansion and multiplication of cells or groups of cells is important in these growth processes. Leaf primordia that are more removed from the apex become progressively larger as they grow outward. The upper or **adaxial surface** of the leaf primordium is directed toward the stem apex, whereas the lower or **abaxial surface** faces away from the side. The resulting **dorsiventral symmetry** is associated with two sides that are morphologically

and anatomically different. In the upward angle or axil (formed by the leaf and petiole with the stem) is a small mound of cells that represents the forerunner of a bud. This is the **axillary bud primordium.** It contains the **axillary meristem,** which when stimulated will give rise to a branch shoot indistinguishable from the primary shoot.

By definition, the **primary body** of the plant and its constituent **primary tissues** include all the tissues that arise more or less directly from the activity of the apical meristems and cell divisions in subapical regions. On the other hand, **lateral meristems,** termed **cambia,** are those regions of dividing cells positioned as a continuous thin sheet on the periphery of the axis, and whose activity is responsible for axis thickness. Lateral meristems participate in **secondary growth** and the formation of **secondary tissues** that will in turn form the **secondary plant body.** The major lateral meristems are the **vascular cambium** that forms

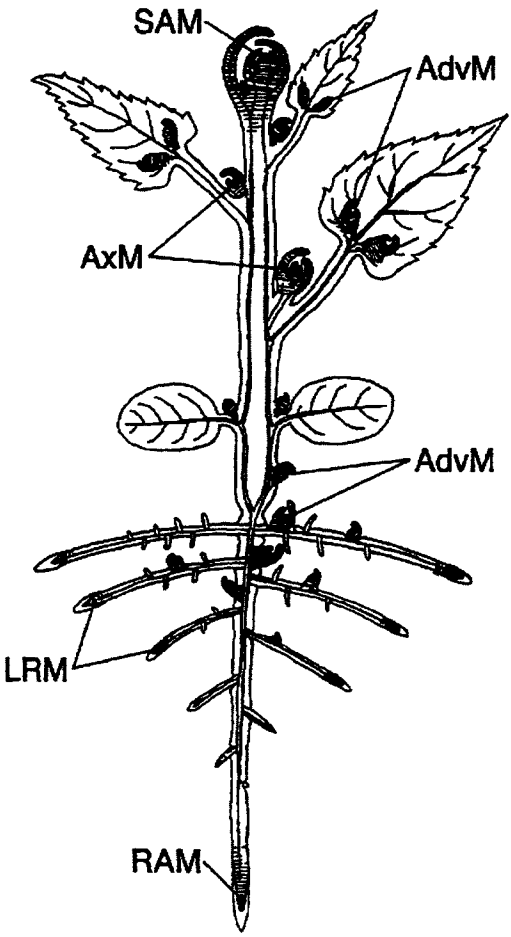

FIGURE 1.1 Vegetative shoot and meristems. An idealized dicotyledonous plant is shown with adventitious buds forming on leaves, roots, and hypocotyl. Abbreviations: AdvM, adventitious meristem; AxM, axillary meristem; LRM, lateral root meristem; RAM, root apical meristem; SAM, shoot apical meristem. Reprinted with permission from Kerstetter and Hake (1997), *Plant Cell* **9**, 1001–1010. Copyright © American Society of Plant Physiologists.

secondary conducting tissues and the **cork cambium** that deposits an outer zone of periderm. A variety of monocots have **intercalary meristems** located at the base of internodal regions. Intercalary meristems produce cells upward into the internode, where they differentiate progressively. There are also specialized meristems such as the so-called **thickening meristem** of some arborescent monocotyledons and various anomalous types of cambial activity.

In woody dicotyledons and all gymnosperms, the region of meristematic tissue positioned between the primary food- and water-conducting cells becomes transformed into the **vascular cambium.** In a narrow sense, the vascular cambium consists of one layer of cells. Each cambial cell divides in a tangential plane to form either a new xylem or phloem mother cell and another meristematic cell. In this way, the vascular cambium is responsible for the increase in diameter of gymnospermous and dicotyledonous roots and stems. The increase in diameter of most monocotyledonous stems and roots results from the enlargement of cells produced in the apical meristem because a vascular cambium is absent in the majority of those plants.

Cell Differentiation

Meristems are composed of two categories of cells, the dividing initials that are capable of proliferation and self-maintenance and the immediate undifferentiated derivatives of cell division that represent the progenitors of the various kinds of cells and tissues possessed by an organ. Under the appropriate influence, these recent derivatives become **differentiated** and changed into various types of mature cells and tissues. From an anatomical point of view, cell differentiation is related to changes in cell size and shape, modifications of the wall, changes in staining characteristics of the nucleus or cytoplasm, as well as the degree of vacuolation and the ultimate loss of the protoplast in some cases. At the subcellular level, major alterations in organelle composition and structure can occur. As cells differentiate, they become specialized to perform a particular function. Generally speaking, the more removed from the embryonic state a cell becomes, the more specialized it is. The mature condition may be irreversible, as in the case of fibers and tracheary elements that have a layered secondary wall and are devoid of a protoplast when functional. In the case of living, nucleated parenchymatous cells, however, the mature condition is potentially reversible, so that a cell retains its capacity for growth and enlargement if subjected to specific influences. If a parenchymatous cell becomes transformed into another cell type without undergoing an intervening cell division, it is said to undergo **transdifferentiation.** When a parenchymatous cell begins to divide and then changes into another cell type, it undergoes **dedifferentiation.**

The transformation of cultured *Zinnia elegans* leaf mesophyll cells into nonliving tracheary elements is an excellent example of transdifferentiation occurring at the cellular level in higher plants. This species is currently being used as an experimental system to study development. Isolated leaf mesophyll cells are induced to differentiate into tracheary elements *in vitro* by stimulation with the appropriate ratio and amounts of the plant hormones auxin and cytokinin. Auxin also plays a role in the differentiation of wound-

induced tracheary elements from parenchymatous elements. The *de novo* origin of adventitious meristems from differentiated tissues provides an example of dedifferentiation.

During the process of differentiation, individual cells or groups of cells undergo **determination,** during which there is a commitment to a particular course of development. As a result, undifferentiated cells assume new identities and eventually become transformed into specialized cells that transport water or food or carry out some other vital function. A cell is considered determined if it has undergone a self-perpetuating change of cytological character states that distinguishes it from other cells and irreversibly commits it to a specialized course of development. Following this definition, a leaf mesophyll cell is differentiated but not strictly determined because its pathway of differentiation is reversible. Water-conducting tracheary cells, on the other hand, become fully determined during their differentiation because they irreversibly enter a differentiation pathway that leads to a dead element.

As tissues mature, certain cells form specific patterns of distribution. The concept of **pattern** refers to the spatial arrangement of elements, in this case cells. The process of patterning involves identifying which undifferentiated cells become transformed into particular mature cell types. It does not include the cytological steps of their differentiation. Cell and tissue patterning is under genetic control and results from complex cell division rates and planes, cell-to-cell communication, and the position of cell types relative to one another.

Determination is a complex and poorly understand process. The structural and physiological characteristics of cells and tissues are the result of a response to a developmental signal (**induction**) and then a commitment to a specific developmental fate. The determined state is expressed in the form of leaf cells, vascular conducting cells, fibers, and so on. This sequence of events is thought to be strongly related to the final position of a cell within the plant and to the position of cells relative to one another. This hypothesis is

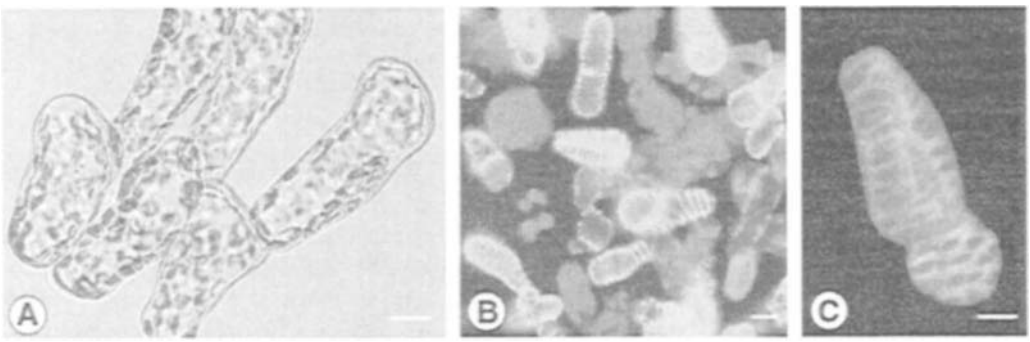

FIGURE 1.2 Morphological changes during tracheary element differentiation in cultured *Zinnia elegans* cells. (A) Isolated leaf mesophyll cells as introduced into culture and observed with phase contrast light microscopy. Scale bar = 10 μm. (B) Cultured cells 96 hr after isolation as viewed with fluorescence microscopy. Differentiated tracheary elements are noted by the yellow autofluorescence from their lignified secondary cell walls. Undifferentiated cells are noted by red autofluorescence from their chloroplasts. Scale bar = 20 μm. (C) Differentiated tracheary cells stained with Calcofluor white to reveal the cellulose-containing secondary cell wall. Scale bar = 10 μm. Courtesy of A. T. Groover and A. S. Jones. (See Color Plate.)

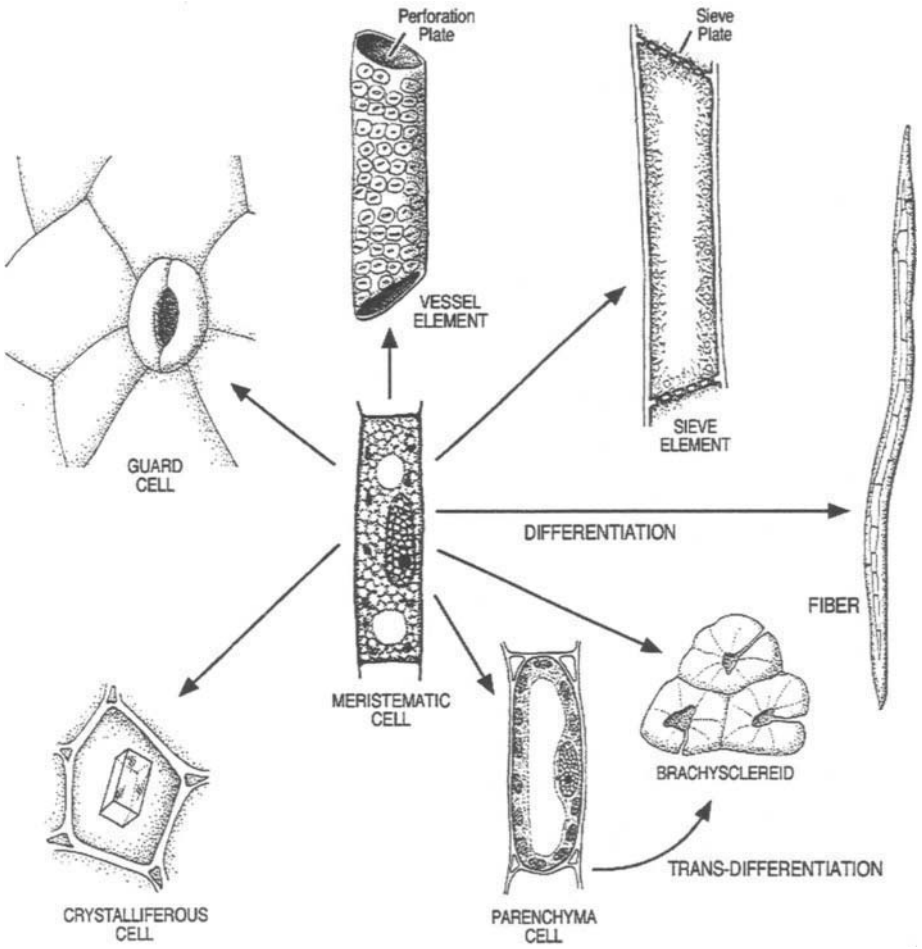

FIGURE 1.3 Representative end products of plant cell differentiation from a meristematic cell. The parenchyma cell retains a living protoplast and is able to transdifferentiate into another cell type, such as a sclereid, that becomes devoid of living contents at maturity.

supported by gene expression patterns and tissue development in plants capable of a specialized type of photosynthesis known as C_4 photosynthesis.

C_4 plants have a distinctive leaf structure, termed **Kranz anatomy**, that involves two major photosynthetic cell types: mesophyll cells that initially absorb the CO_2 entering the leaf through the stomata, and bundle sheath cells that immediately surround the veins and collect CO_2 from the mesophyll. Sugars are manufactured within the latter cells and are then transported into the conducting phloem. Evidence indicates that these two closely spaced and interacting cell types interpret positional information that is distributed around each vein to express cell-specific genes correctly during the differentiation of the Kranz pattern. The fact that position-dependent information is essential in establishing cell fate also has been documented in experiments performed on developing roots. If an epidermal initial cell is removed, the under-

lying cortical cell alters its course of differentiation and becomes transformed into an epidermal cell. If a cortical cell initial is removed, an underlying pericycle cell replaces the missing cell. It has been hypothesized that daughter cells within the root apex produce positional signals that control cell fate.

The morphogenetic signals that control development are largely unknown. They lie at the heart of some of the most difficult, unsolved problems of morphogenesis. How do cells receive positional information from their neighbors and how does this information initiate the events leading to cell differentiation? One possibility involves a functional connection between the plasma membrane and the cell wall substrate. Surface adhesions may form interactive networks that are involved in the perception and movement of positional information. Such networks then may function directly in sensing the environment, polarity, tropic movement, and differentiation. It is important to emphasize that plant cells are not mobile and that their position is fixed at the time of cell division. In plants, therefore, there are none of the complexities of cell mobility and adhesion that result in different morphogenetic phenomena in animals. However, plant cells do undergo considerable enlargement during the differentiation process, and this may produce cell displacement, intercellular spaces, and particular cell arrangements. As a consequence of the lack of plant cell mobility, cell position appears to be more important than cell lineage in influencing the direction of plant cell maturation.

A complete understanding of the patterns and underlying causes of cellular determination and differentiation, as well as the origin, development, and structural modifications of divergent organs, remains a major challenge to plant scientists. In recent years, the concept of **heterochrony** (changes in developmental timing) has been advocated as a major influence on the evolutionary change in plant and organ form. However, in order to understand how tissues arise (**histogenesis**) and organs develop (**organogenesis**), it will be necessary in subsequent chapters to clarify the remarkable structural characteristics of vegetative meristems and how they function.

TERMS USED IN THE DESCRIPTION OF PLANT CELLS

The minute, careful, and at times even tedious observations and descriptions that form the bases of plant anatomical study require an understanding of basic terminology denoting cellular orientation. The terms "transverse," "axial," "radial," and "tangential" are used to describe cell and tissue surfaces in sectioned tissues with reference to the long axis of the stem, branch, or root. A **transverse section** or wall (also known as a transection or cross section) pertains to the side perpendicular to the longitudinal axis. A **radial** (or axial) **section** or cell wall is a longitudinal surface along a radius of the axis. A **tangential section** or cell wall refers to a longitudinal surface at right angles to an axis radius. Cell orientation in relation to the long axis may not be clear or may be descriptively unimportant for individual cells, as, for example, when the cells of a tissue become disassociated into a **maceration** of separate cells. Here the terms "end wall" and "longitudinal wall" or "lateral wall" are most often used in relation to the long axis of the cell.