SECTION

I

SOME SPECIAL ASPECTS OF PLANT GROWTH AND DEVELOPMENT

The chapters in Section I of this book are designed to serve two purposes. First, to highlight the fact that plants, while sharing many building blocks and metabolic pathways with animals, nonetheless are organized along different lines and have adopted different strategies for survival. Second, the chapters provide a backdrop for topics covered in Sections III and V, which deal with hormonal and environmental regulation of plant growth. Chapter 1 describes the basic organization and development of an angiospermous plant. Chapter 2 is devoted to a discussion of the structure of cell wall and its importance, the major features of cell cycle and cell division in plants, and types of cell growth. Chapter 3 highlights patterning in zygotic embryo development and discusses somatic embryogenesis, an ability that plants have as a result of open growth and open differentiation. Chapter 4 deals with the question of determination, differentiation, and dedifferentiation in plants in the context of the inherent plasticity of plant development. An Appendix on molecular and genetic techniques used for the study of plant development concludes Section I.

CHAPTER

1

Special Features of Plant Development

1. PLANTS HAVE EVOLVED SOME NOVEL STRATEGIES FOR SURVIVAL

Plants are rooted to soil and hence have evolved several strategies for survival that are absent or unheard of in animal life. Nowhere are these strategies more clearly evident than in the manner in which the plants grow and their cells and tissues differentiate.

1.1. Plants Show an Open Form of Growth

Plants are unique multicellular organisms that retain the capacity for unlimited growth, that is an overall increase in size, throughout their lives. They are able to do so because they have **meristems** at certain locations in the body. Meristems are composed of stem cells, which perpetuate themselves by cell divisions and also give rise to derivative cells, which differentiate along new lines. As a result of meristematic activity, fresh quotas of tissues and organs are formed, and the plant continues to grow in height and, in many cases, girth throughout its life. This form of growth in plants is referred to as an **open form of growth**. The advantages to this type of growth for organisms that are rooted but subject to predation are immediately obvious.

In contrast, in most animals the adult life is characterized by a cessation of growth, except in some instances where regeneration of an organ or body part occurs. While overall growth stops in animals, cell divisions and a turnover of cell populations may continue in stem cells at several locations and add new derivatives. In contrast, in plants, a turnover of cells in mature tissues is rare.

Plant meristems are classified on the basis of location (Fig. 1-1). **Apical meristems** are located at or near the tip of shoot or root and are called shoot and root apical meristems; they are responsible for primary growth, including elongation growth, of these organs. **Lateral meristems**, e.g., vascular cambium, cork cambium, are

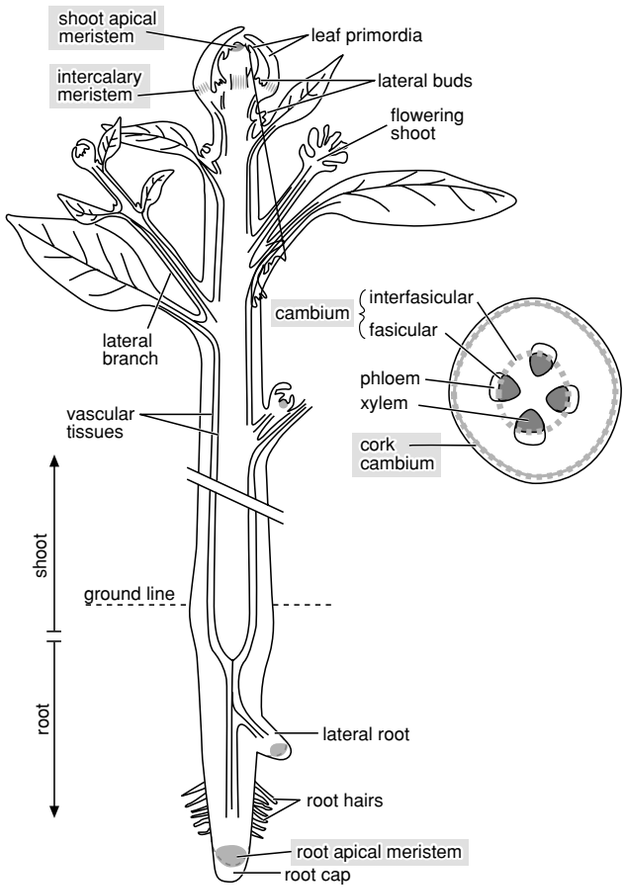


FIGURE 1-1 Diagrammatic representations of a dicot plant showing the principal meristems. Shoot and root apical meristems are indeterminate meristems—they continue to produce new shoot and root tissues throughout the life of the plant. In contrast, leaf and flower development involves meristems that function only for a defined duration—they are examples of determinate meristems. Intercalary meristems typically occur in grass stems and leaves, but are shown here to denote their locations. In dicots and gymnosperms, a vascular cambium originates in parts that have ceased elongation. In stems, it originates between primary xylem and primary phloem in a vascular bundle, or fasicle, and extends to the interfasicular areas, thus establishing a complete cambial ring. In roots, it arises slightly differently, but eventually forms a complete ring. In older roots and stems, the epidermis cannot keep pace with increasing girth and is replaced by a new tissue called periderm. Periderm owes its origin to a new meristem, called cork cambium or phellogen.

located on the sides of roots or stems and add to the girth, or secondary growth, of these organs. **Intercalary meristems** typically occur intercalated between mature regions, as at the bases of grass leaves; however, in a broader sense, they can be considered to occur at the bases of leaf primordia and above the nodes in stems of nearly all plants and add to elongation growth of these organs. Meristems are also classified as **indeterminate** and **determinate**. Shoot and root apical meristems (although not necessarily the same meristem), and vascular cambium, remain active for the life of the plant; hence, they are referred to as indeterminate meristems. In contrast, meristems involved in leaf and flower development are active only for a short time and are used up in the formation of those organs; in some texts, they are referred to as determinate meristems.

1.2. Structural Support for the Plant Body Is Provided by Cell Walls

Plants absorb water and minerals from soil, CO_2 and O_2 from air, carry on photosynthesis, transport photoassimilates to growing parts where they are used for growth, store photoassimilates as food reserves (carbohydrates, proteins, lipids), reproduce, and eventually die. Because they are rooted, they have to grow continuously to search for new sources of water and minerals as well as compete against neighbors for light. Root and shoot apical meristems provide for this growth. In some cases, because of the activity of the apical and lateral meristems, they grow to phenomenal sizes, e.g., redwoods, eucalyptus, and banyan tree, and live to be 3000–4000 years old, e.g., bristle cone pine. Structural support for the plant body is made possible by the presence of cell walls. In young organs, turgor pressure inside cells also contributes to structural support. The presence of a cell wall is a mechanical necessity for plants because it provides rigidity and strength while allowing flexibility, but it also imposes major restrictions to cell growth. A study of the chemical composition and architecture of cell walls, therefore, is essential for understanding both cell division and cell growth in plants (see Chapter 2).

1.3. Plants Development Is Highly Plastic

Being rooted, plants have evolved to perceive environmental factors, such as light, gravity, temperature, water, and touch. These environmental stimuli are perceived, sometimes with exquisite precision, and a response is affected in terms of growth, differentiation, reproduction, and so on. Plant development, as in all organisms, is basically regulated by its genetic complement, but, in contrast to multicellular animals, it is also characterized by extreme plasticity. **Plasticity** is a term used to describe the ability to change form or shape in response to a change in environment; no genetic change is involved. This is illustrated by two examples.

Many aquatic or semiaquatic plants show the phenomenon of heterophylly, which is the production of two or more forms of leaves within the same individual. The buttercup, yellow water crowfoot (*Ranunculus flabellaris*), produces leaves that have three broad lobes,

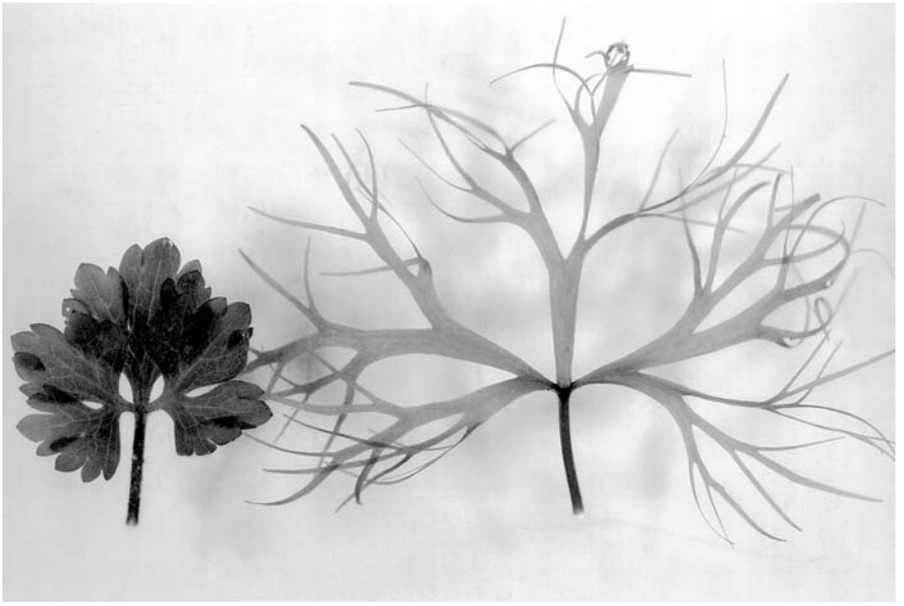


FIGURE 1-2 Heterophylly in buttercup, *Ranunculus flabellaris*. A leaf produced while the shoot apex was in air (left) and while it was under water (right). Courtesy of Michelle Woodvine and Nancy Dengler, University of Toronto, Toronto.

each lobe with one deep and several shallow sinuses, when exposed to air, but when submerged produces leaves that are highly dissected and filamentous (Fig. 1-2). The change in leaf form extends to changes in leaf anatomy and stomata. It should be noted that it is only the new leaves that are produced at the shoot apex subsequent to submergence that are dissected and filamentous—leaves that were produced before submergence do not change shape.

Seedlings of most dicots grown in the dark have long, spindly, yellow stems with small enation-like leaves at nodes, whereas those grown in light have robust, although shorter, green stems and well-expanded leaves. The change from a dark-grown to a light-grown phenotype is dramatic and affects not only internode length, leaf form, and chlorophyll synthesis, but also many other features.

Except for light, the perception of environmental signals, or receptors for environmental signals, are not always clear or known; in fact, very little is known about them, but the signaling pathway in many cases involves hormones.

1.4. Plants Show Open Differentiation

Plant cells and tissues differentiate to perform specific functions, but under certain circumstances they retain the ability to revert to an earlier state and go off in a new direction. This ability is referred to as open differentiation and is dealt with in Section 5 of this chapter. The plasticity of plant growth is possible because of both open growth and open differentiation.

2. GROWTH, DIFFERENTIATION, AND MORPHOGENESIS

Growth of an organism is defined as an irreversible increase in mass. Because mass is related to cell volume and cell number, growth refers to an irreversible increase in cell size (enlargement) or to an increase in cell size as well as cell number (cell division). Cell division, by itself, is not sufficient to result in growth. **Differentiation**, in contrast, refers to the acquisition of qualitative differences among cells of common ancestry, i.e., those derived from a cell or group of cells. It is by differentiation that cells in an organ or tissue become different from each other, or specialized for different functions, e.g., the epidermis, or mesophyll, or xylem or phloem cells in a leaf. From a functional viewpoint, differentiation is equivalent to specialization. **Morphogenesis** is the acquisition of form, how a plant or organ acquires its distinctive shape or form. Because plant cells, generally, are fixed in relation to each other and because they are cemented by the cell wall (they are not free to move about as in animal development), morphogenesis in plants is essentially a function of planes of cell divisions and direction of cell growth. The control of these two processes, therefore, is central to a study of plant morphogenesis.

The basic features of cell division and cell growth are dealt with in Chapter 2, following a discussion of the composition and structure of the cell wall. Hormonal regulation of cell division and cell growth is covered in Chapter 15.

3. ORGANIZATION OF THE PLANT BODY

3.1. Embryo Development in Angiosperms

All multicellular plants arise from a single cell, the fertilized egg or **zygote**. A series of cell divisions in the zygote, followed by differentiation, set out the pattern for the embryo, which, if undisturbed, lasts throughout the life of the plant.

Embryo development in vascular plants, which include club mosses, horsetails, ferns, gymnosperms, and angiosperms, varies considerably. This section considers the typical embryo development in angiosperms. For other groups of vascular plants and for variations among angiosperms, the reader is referred to the excellent texts by Steeves and Sussex (1989) and Johri *et al. (1992).*

In angiosperms, the first division of the zygote is often, although not always, asymmetric and sets up an **apical** cell toward the chalazal end and a **basal** cell toward the micropylar end of the ovule (Fig. 1-3). The apical cell is smaller and densely cytoplasmic, whereas the basal cell is larger and has a big vacuole. These are only the most obvious differences between these two cells; at the cytoskeletal and especially biochemical level, there must be many other differences, although they still need elucidation. The fates of these two cells are dramatically different.

Divisions in the apical cell give rise to the embryo proper, which goes through several, but continuous, developmental stages, an eight-celled **proembryo** is followed by **globular**, **heart-shaped**, and **torpedo** stages (Fig. 1-3). The body plan of the embryo, i.e., the setting out of the **root** and **shoot poles**, **root–shoot axis**, and **cotyledons**, is evident between heart and torpedo stages. ''Relatively uncommitted'' (see Section 4.2.1 in this chapter; also, Chapter 4) groups of cells at the root and shoot poles become the future **root** and **shoot apices** with their own distinctive organizations. Embryonic tissues are also distinguished very early. A **protoderm** is evident already in the globular embryo, and the **ground meristem** and **procambium** become distinguished in the heart-shaped embryo. Further growth of the embryo continues for some time by cell division and cell enlargement, but eventually growth ceases and the embryo enters a period of quiescence; further growth occurs only after germination. In many cases, because of the limited space within the ovule, now the seed, the embryo bends over on itself.

The basal cell divides to give rise to a structure known as the **suspensor**, which varies in size, from small and filamentous to massive, and which is believed to anchor the embryo in its proper position in the developing seed. The development of the suspensor generally precedes that of the embryo proper, and there is evidence that the suspensor serves to provide nutrition and hormones to the very young embryo. Some of these substances may be transported from the mother plant, whereas others are synthesized *in situ* in suspensor cells (see also Chapter 18). After the globular stage, the suspensor often shrivels up and becomes nonfunctional. While most of the suspensor is distinct from the embryo proper, the part proximal to the embryo, the **hypophysis**, contributes to the root apex.

The description just given pertains to most dicot embryos, but there are exceptions. For example, the setting out of the embryo proper and the suspensor is not always traceable to the first division of the zygote, although it occurs early on. Also, the subsequent divisions may not be as regular as those described, although ultimately the major organs and tissues are formed in expected places.

The embryo development in dicots and monocots is similar to the globular stage, but later in dicots the shoot apex develops along the same axis as the root apex and the two cotyledons occur laterally; whereas in monocots, the shoot apex occupies a lateral position and the single cotyledon is more terminal (Fig. 1-3k). This seemingly minor difference in embryo development between these two classes of flowering plants has enormous taxonomic significance and became established very early in the origin of flowering plants.

How do apical and basal cells come to have divergent destinies? What is the basis for the orderly unfolding of the embryonic pattern? How are the root–shoot polarities established? The answers to these questions are still largely unknown. However, application of molecular genetic techniques to analysis of pattern formation, improvements in techniques of isolating very young embryos and their *in vitro* culture, isolation of embryo sac and egg cell and *in vitro* fertilization, and mass production of somatic embryos at nearly synchronous stages hold great promise that environmental factors, including maternal signals, if any, that set up these patterns and polarities will soon be revealed.

We will go into some of this literature in Chapter 3. This section continues with organization of the adult plant body.

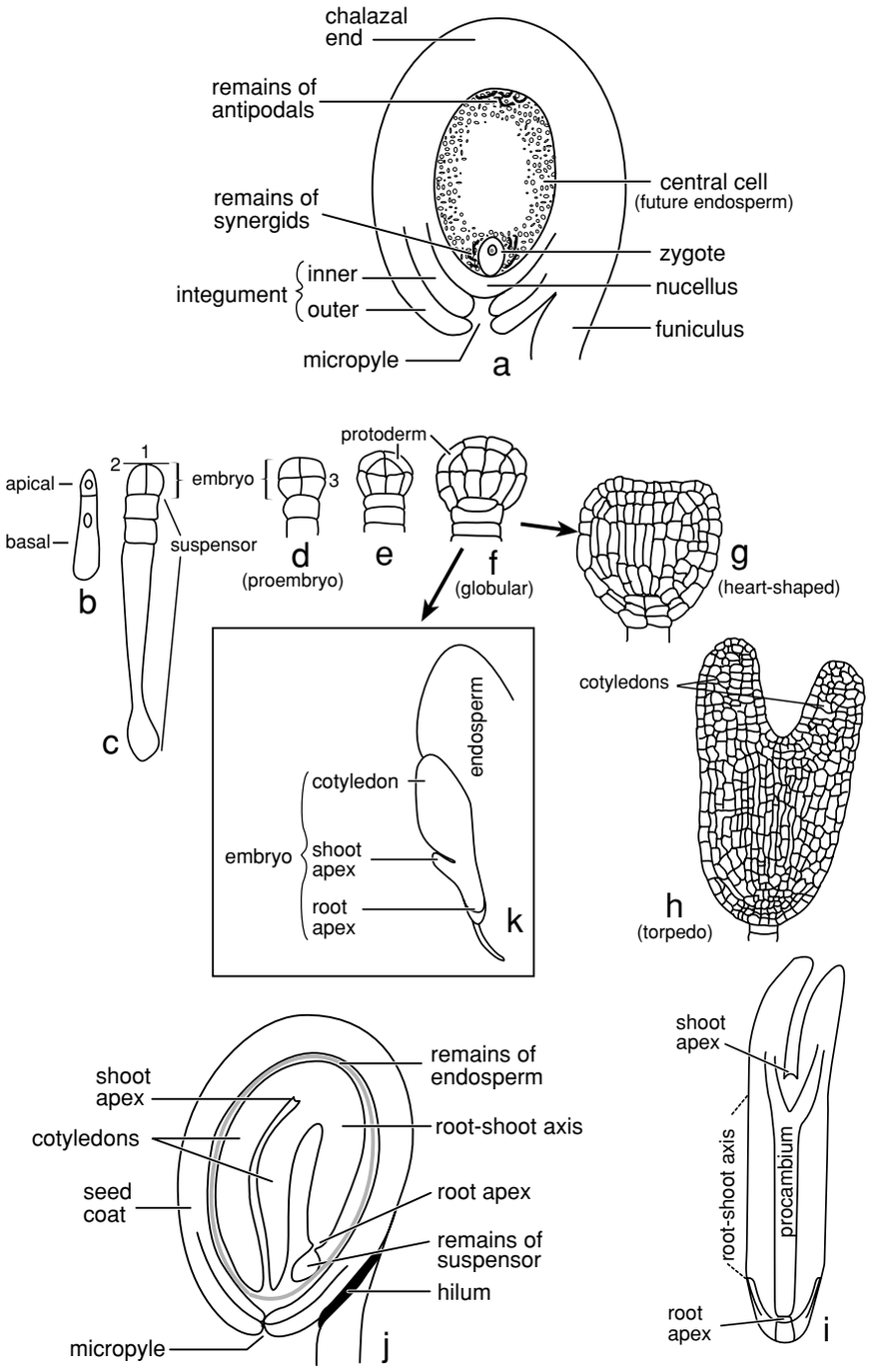


FIGURE 1-3 Stages in embryo development in a typical angiosperm. (a) An ovule after fertilization with the inner and outer integuments (which later form the seed coat), the micropyle, the chalazal end, and the central cell (formerly the embryo sac) with the zygote and several endosperm nuclei. The ovule is attached to the placenta in the ovary *via* a funiculus. (b and c) The first division of the zygote sets out apical (toward the chalaza) and basal (toward the micropyle) cells, which give rise to the embryo proper and the suspensor, respectively. The first three divisions in the apical cell, which give rise to the eight-celled proembryo, are numbered. (d–h) The embryo goes through several developmental stages, an eight-celled proembryo (d), globular (e and f), heart-shaped (g), and torpedo (h) stages. A protoderm is evident in the globular embryo, and the ground meristem and procambium become distinguished in the heart-shaped embryo. Cotyledons and a root–shoot axis become evident between heart and torpedo stages. The suspensor is not shown in these stages, it usually degenerates by the globular stage embryo. (i and j) Enlargement of the embryo continues for some more time, but eventually ceases; further growth is resumed only after germination. Because of the limited space, the embryo in some cases bends

3.2. The Adult Body

3.2.1. The Root Apex

The root and shoot poles established in the transition from heart- to torpedo-shaped embryo become organized as the root and shoot apices with their own distinctive structure, patterns of division, and the nature of derivatives. The **root apex** is responsible for the orderly growth of roots, whereas the **shoot apex** is responsible for the orderly growth of stems, as well as the initiation of new leaves, branches, and flowers.

The two apices are organized along different lines (cf. Figs. 1-4 and 1-8A). In most roots, the root apical meristem is not terminal but subterminal and is covered over by a structure known as the **root cap** (Fig. 1-4). The root cap serves some very useful functions for the plant. It is important in the perception of gravity such that roots grow toward the earth. It protects the apical meristem from abrasion during growth through the soil. The outer cells of the root cap keep getting sloughed off as new cells are added from within by the root apical meristem. It also secretes various types of compounds; mucilage, which facilitates the passage of root through the soil, and other carbohydrates and phenolics, which are important in interactions of plant root with microbes and fungi in the rhizosphere.

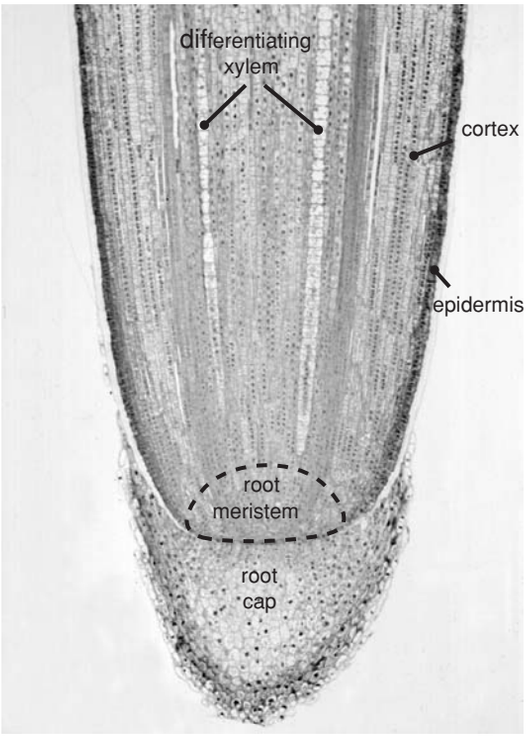


FIGURE 1-4 Longitudinal section of a maize (*Zea mays*) root showing the root apical meristem and the root cap. The section passes through parts of two longitudinal files of differentiating xylem cells.

Cell divisions occur throughout the apical meristem, although a group of cells in the middle, the so-called **quiescent center**, divides much less frequently than others at the periphery. This can be shown by feeding radioactive thymidine to growing roots. The radioactive thymidine gets incorporated into DNA of dividing cells and the radioactivity can be visualized on an X-ray film (Fig. 1-5A). For quantitative measurements, the frequency of cell divisions in different parts of the root apex is calculated by counting the number of mitotic figures in sections of roots sampled over a defined time interval, but this a more laborious process (Fig. 1-5B).

The divisions in the apical meristem add new cells both acropetally to the root cap and basipetally to the zone of elongation and differentiation. In this latter zone, component cells continue to divide; they elongate as well, such that the whole organ elongates. Also, various tissue types, epidermis, cortex, endodermis, xylem, and phloem, begin to differentiate (Fig. 1-6). As a result of this elongation, the root tip is constantly pushed downward into the soil. Further basipetally, elongation gradually comes to a stop, whereas individual cell and tissue types, especially xylem elements, complete their differentiation and mature. In this zone of maturation, certain epidermal cells give rise to **root hairs**, which enhance the surface area of epidermal cells several fold and thus help in the absorption of water and minerals from the soil. **Endodermal cells**, with their specialized Casparian strip (or band), are involved in selective screening in the uptake of minerals and are well differentiated in the root hair zone.

In the region that is no longer involved in extension (or elongation) growth, **lateral roots** arise by localized divisions in the pericycle (Fig. 1-7). The nascent root primordium (primordium = a developing unit) grows through the cortex and epidermis of the parent root to emerge as a new lateral root. Lateral roots have a similar organization as the parent root and serve likewise for

over on itself. This period of enlargement is accompanied by reserve food deposition. In some seeds, the endosperm gets used up during this period, and the food reserves are deposited in the cotyledons and the root–shoot axis (see j); in others, the endosperm persists and is the main site of food deposition. (k) Embryo development in monocots is similar to that in dicots to the globular stage. Subsequently, in monocots, the shoot pole arises not in a straight line with the root pole, but laterally, and the single cotyledon occupies a more terminal position. Adapted from West and Harada (1993).

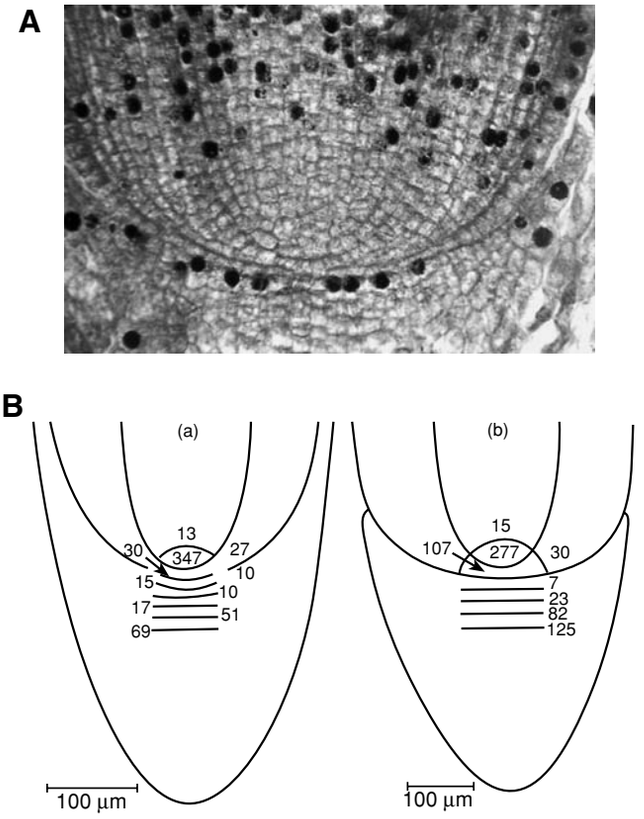


FIGURE 1-5 Cell divisions in the quiescent center and peripheral regions of root meristem. (A) Radioactive thymidine treatment of maize (*Zea mays*) roots. Cells in the peripheral parts of the root meristem show a greater incorporation of the radiolabel, which means that they are dividing more rapidly than those in the quiescent center. (B) Cell doubling time in hours in different parts of sunflower (*Helianthus anuus*) and maize roots. To calculate these times, root tips are sampled at intervals over a defined time period, sectioned, and examined for mitotic figures (colchicine is used to accumulate cells in metaphase). A large number of root tips in each sample provides statistically reliable counts [A, courtesy of Lew Feldman, U.C. Berkeley; B, with permission from Furuya (1984), © Annual Reviews].

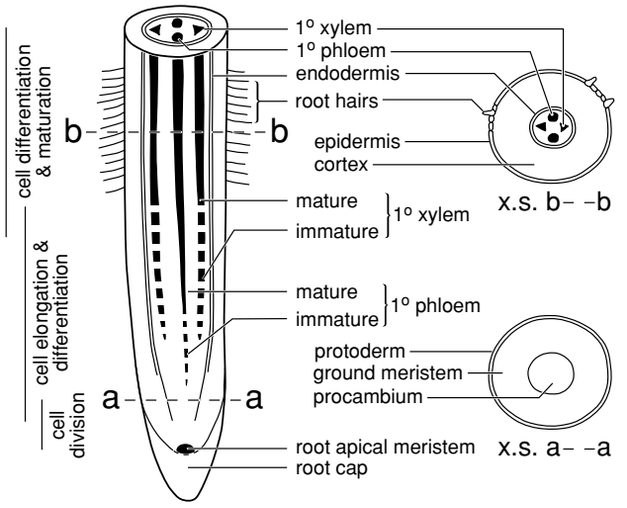


FIGURE 1-6 Diagrammatic illustration of growth and cell differentiation in a dicot root. The root tip is divided roughly into three zones on the basis of primary activities: cell division, cell elongation and differentiation, and cell differentiation and maturation. The zones partially overlap. Basipetally from the apical meristem, three primary tissues, protoderm (which gives rise to epidermis), ground meristem (which gives rise to cortex and endodermis), and procambium (which gives rise to xylem, phloem, and pericycle), are demarcated (see cross section at level a–a). Further basipetally, root elongation ceases and tissues and cell types mature. The cross section at level b–b shows all the primary tissues, epidermis (shown partly cellular to illustrate that root hairs are outgrowths of epidermal cells), cortex, endodermis, pericycle, primary (1°) xylem, and primary (1°) phloem.

both anchorage and absorption of water and minerals. In roots of woody dicots and gymnosperms, the vascular cambium is also initiated in the region, which is no longer elongating. The vascular cambium divides periclinally and produces secondary xylem and phloem.

3.2.2. Shoot Apex, Leaf Development, and Flowering Apex

The shoot and shoot apex are organized along entirely different lines from the root and root apex (Fig. 1-8A). The term **shoot** is used to denote stem and leaves together—the development of these two organs is inextricably linked and traceable to the shoot apex. The apex of the stem is covered over by a series of **leaf primordia**, with the youngest primordium being closest to the apex. To see an apex, these primordia must be surgically removed under a dissecting scope. A longitudinal section through the apex, with all but the youngest few leaf primordia removed, shows an apical meristem, which, depending on the species, may be dome shaped, conical, flat, or even concave. The term **shoot apex** is an inclusive term, whereas **shoot apical meristem** (SAM, or shoot meristem), by definition, is the part of the shoot apex above the youngest, discernible leaf primordium. In most flowering plants the shoot meristem shows an organization into a **tunica** and **corpus** [in gymnosperms and ferns, the apical organization is different, see Steeves and Sussex (1989) for details]. The tunica consists of one to several layers of cells at the periphery that divide predominantly in an **anticlinal plane**, i.e., at right angles to the surface; corpus cells, in contrast, divide in all planes (Fig. 1-8B).

Tunica and corpus refer to the organization of the apex. They do not give an indication of the frequency or site of cell divisions. As in the root apex, the central part of the shoot apical meristem, referred to as the **central zone**, is a region of low mitotic activity (Fig. 1-8C). The cells in this region, usually few in number, divide

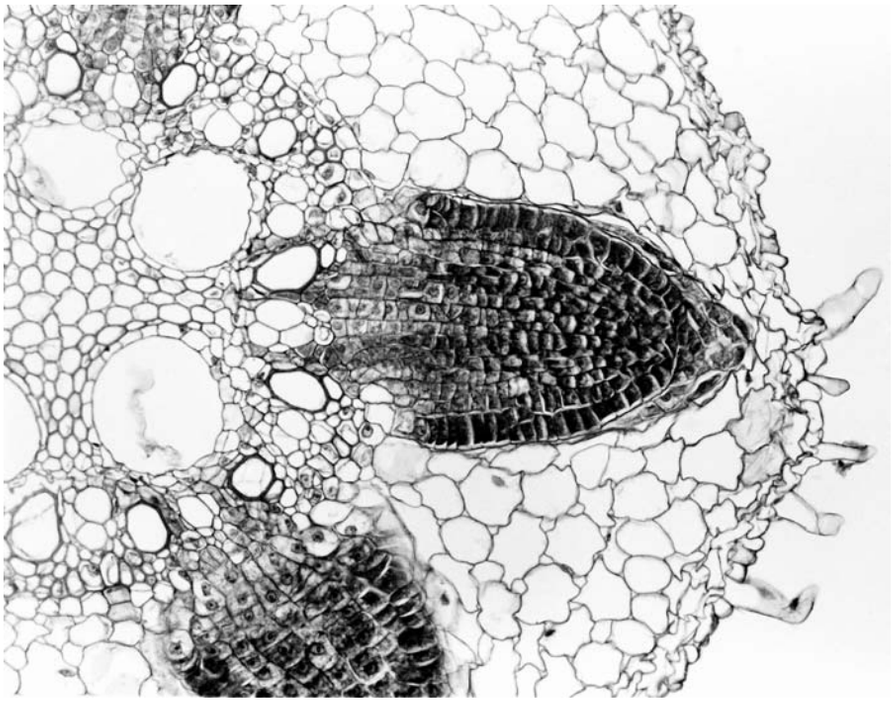


FIGURE 1-7 Origin of lateral root in maize (*Zea mays*). Lateral roots arise in the pericycle and grow through the cortex and epidermis of the parent root. Courtesy of Nancy Dengler, University of Toronto, Toronto.

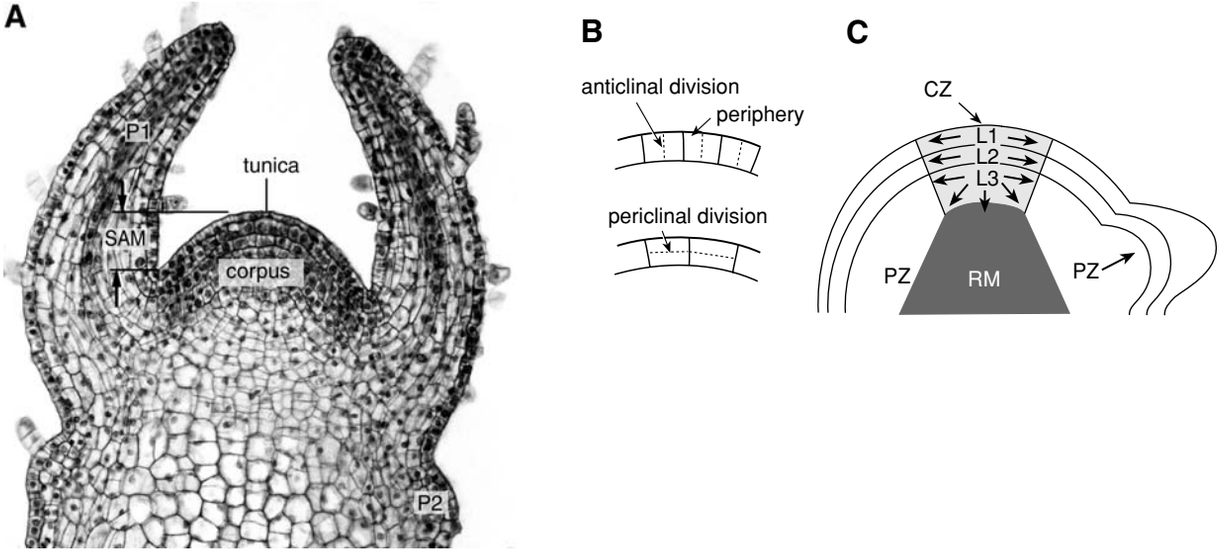


FIGURE 1-8 (A) Longitudinal section of the shoot apex of *Coleus*. The part above the youngest leaf primordium is considered the shoot apical meristem (SAM). It shows tunica layers surrounding a central mass of cells known as corpus. In *Coleus*, leaves are borne in an opposite decussate manner, which means that each succeeding pair of opposite leaves arises at right angles to the previous pair. The section passes through parts of two pairs of leaf primordia or young leaves (P1 and P2): P1, the youngest pair, is seen arching over the shoot meristem, whereas the P2 pair is seen as small protuberances (due to the plane of section) on the two sides of the stem. Trichomes (hairy outgrowths) are seen arising from the epidermis of P1. (B) Anticlinical and periclinal divisions. Cell divisions that are parallel to the periphery of root or stem are called periclinal divisions, whereas those that occur at right angles to the periphery are called anticlinal divisions. (C) Line sketch of a shoot apex showing the location of the central zone (CZ), peripheral zone (PZ), and the rib meristem (RM). Surface and subsurface layers are designated L1, L2, and L3. The CZ contributes cells to the surrounding ring of cells in the PZ as well as the RM below [A, courtesy of Nancy Dengler, University of Toronto, Toronto; C, from Liljegren and Yanofsky (1995) with permission from Elsevier Science].

slowly and give rise to cells below and on the sides to give rise to the **rib meristem** and the **peripheral zone**, respectively. Cell divisions occur mostly in localized areas in the peripheral zone, where lateral organs, such as leaves, are initiated, and in the rib meristem, which contributes to internodal elongation. The surface and subepidermal layers are designated L1, L2, and L3. L1 and L2 usually divide anticlinally, whereas L3 divides both anticlinally and periclinally. L1 and L2, and in most cases L3 as well, are continued into lateral organs and contribute to various tissues in these organs to varying extents.

3.2.2.1. Leaf Development

Leaves are highly plastic organs and show a great variety of form and size. Typical leaves are flat, dorsoventral organs adapted for photosynthesis. Their arrangement on the shoot, known as phyllotaxy, is specific for each species. Knowing the phyllotaxy, one can predict with considerable accuracy where the future leaf, or leaves, would arise on the shoot apex.

Much of our recent information on leaf development in flowering plants has come from a study of cell lineages in genetic mosaics. Genetic mosaic, as the term implies, means an organ (or organism) that is composed of cells of more than one genotype. For studies in plant development, genetic mosaics are obtained in two ways: In periclinal chimeras, one or another cell in the outer surface (L1) or subsurface (L2 or L3) layers in the shoot meristem (usually CZ), shows a stable genetic change, the change spreads throughout the layer, and is perpetuated in subsequently produced lateral organs or axillary buds. The change itself may be chemically induced, e.g., polyploidy after colchicine treatment, or a natural mutation or it may be due to a graft from a different plant, but as long as it can be seen with naked eye or under the microscope, it serves its purpose. In clonal analysis, embryos in immature or mature seeds or seedlings may be mutagenized using ionizing radiation. As a result, some cells in the shoot apex or young leaf primordia may be mutagenized. These cells, when they divide subsequently, leave a record of their progeny (or clone). If the mutation is in some visible marker, e.g., loss of synthesis of chlorophyll or pigments such as anthocyanin, the clones can be easily followed during development.

These studies have revealed that the origin of most lateral organs can be traced to groups of cells, called **founder cells**, at the periphery of the shoot meristem. The group of cells spans all three layers of the meristem: L1, L2, and L3. For leaf development, the number of cells may range from about 5 to 10 cells per layer in *Arabidopsis* to somewhere between 50 to 100 cells per layer in tobacco, cotton, and maize.

The initiation of a leaf is signaled by the onset of a few periclinal divisions in the outer surface and subsurface layers of the founder group, accompanied by a change in the orientation of growth. As a result, a bulge or leaf buttress is formed, which with continued growth gives rise to a leaf primordium. In dicots, the primordium often has a flat surface toward the shoot apex and a curved surface on the opposite side (Fig. 1-9). Subsequent growth of the primordium involves elongation by intercalary growth and growth at the margins to form a flat lamina, or blade. In grasses, leaf initiation follows a slightly different course. Mitotic activity in the founder cells spreads in the peripheral zone almost surrounding the shoot meristem before elongation growth starts. Thus, a hood-like primordium results and a sheathing leaf base is formed.

Subsequent leaf development is often analyzed in terms of three axes, which define the major parts of the leaf, its eventual shape, and the major tissue layers (see line drawing in Fig. 1-9B). The apical/basal axis defines the extent of the leaf blade (or lamina), which develops distally, and the petiole, leaf base, or leaf sheath, which develop proximally. The centrolateral axis defines the midrib and the lateral extent of the lamina. The dorsoventral (or the adaxial/upper and abaxial/lower) axis defines the extent of major tissues through the width of the leaf. All three layers participate to varying extents. L1 forms the epidermis, L2 gives rise to the inner subdermal layers, including upper and lower mesophyll, and L3 the innermost layers of mesophyll and vascular tissues (Fig. 1-10). Some inner tissues may be of mixed origin from L2 and L3. These definitions proceed with both cell divisions and differential cell expansion and lead to production of a fully mature leaf.

An important point to note here is that, in dicots and most monocots, although meristematic activity occurs in the leaf primordium and through most of leaf development, sooner or later it comes to a close—the meristematic potential of the primordium is used up during leaf development. Thus, while shoot (or root) apical meristems are indeterminate in nature, leaf meristems are determinate and leaf is a determinate organ. In grasses, an intercalary meristem at the base of the leaf continues to add new leaf tissue indefinitely, while the older, more distal parts differentiate and mature. Thus, it is that grass can be mowed.

3.2.2.2. Internodal Elongation

The site at which a leaf is initiated is designated a **node**; the intervening stem segment between two nodes is an **internode**. Cells in the ground tissue above each node, derived from the CZ (see Fig. 1-8C), divide

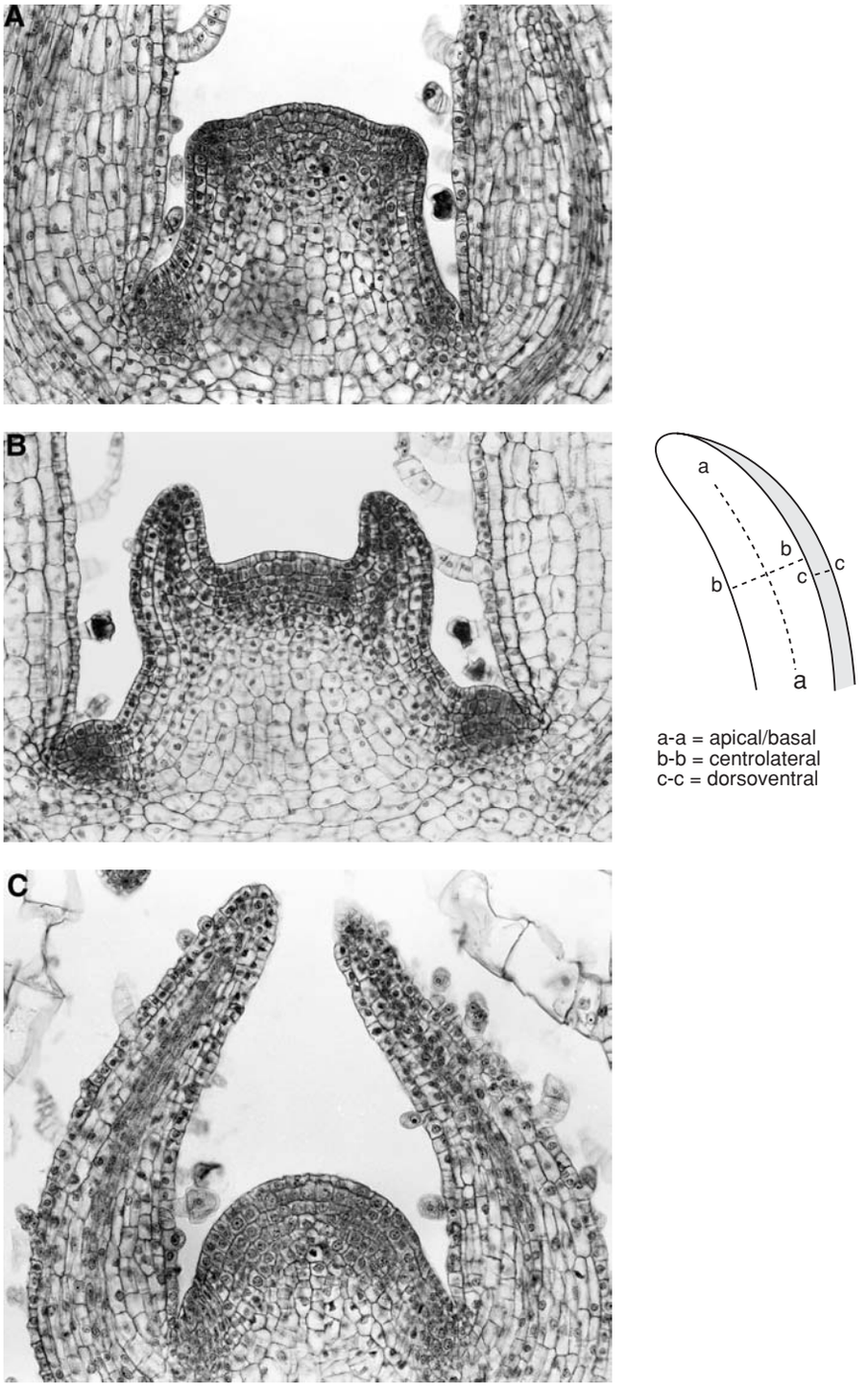


FIGURE 1-9 Leaf development in *Coleus*. Three stages in leaf development are shown. (A) A pair of very young primordia. (B) A slightly later stage. The accompanying line drawing shows the three axes of growth. (C) A pair of young expanding leaves with most of the major tissues and cell types defined. Courtesy of Nancy Dengler, University of Toronto, Toronto.

preeminently in a transverse plane, resulting in longitudinal files or ribs of cells, referred to as **rib meristem** (Fig. 1-11A). Cells derived from this activity elongate, resulting in growth in length of the internode. In most plants, such extension growth continues over several internodes below the apical meristem. As a result

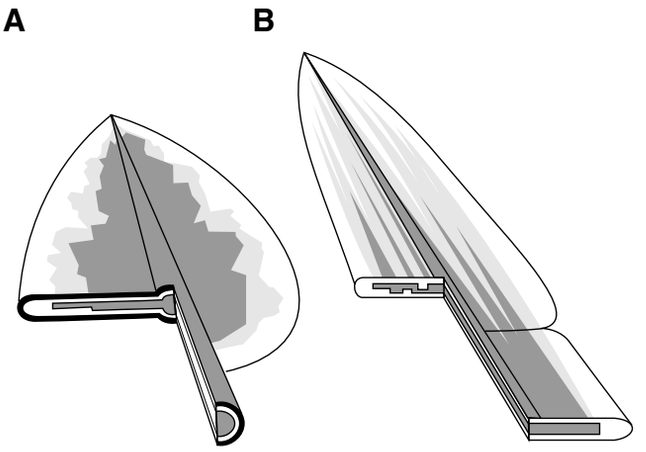


FIGURE 1-10 Distribution of tissues derived from L1, L2, and L3 layers of the shoot apical meristem in a tobacco leaf and a maize leaf. (A) A leaf from a green (L1)–white (L2)–green (L3) periclinal tobacco chimera. In tobacco, the L1 lineage is confined to the epidermis. Most of the tissue at the margin of the leaf is derived from the L2 lineage because of periclinal divisions in this layer early in the expansion of the lamina. (B) A leaf from a white (L1)–green (L2)–green (L3) periclinal maize chimera. In maize, the L1 layer produces epidermis, plus all of the tissue at the margin of the leaf, whereas the L3 layer produces little, if any, of the tissues in the lamina. From Poethig (1997).

of this elongation, the shoot apex and the young leaf primordia are constantly carried upward. Sooner or later, however, the older internodes cease elongation. Thus, the primary extension or elongation growth of the stem occurs only in a few internodes below the apical meristem; the rest of the stem does not elongate. There are some plants, such as celery, lettuce, and cabbage, where the leaves and shoot apex stay close to the ground, because while the leaves are initiated and formed, internodal elongation below the apical meristem is suppressed. These plants are called **rosette** plants. Likewise, in many dwarf varieties of wheat, maize, and pea, which are genetic mutants, the internodal elongation is severely curtailed.

Differentiation of primary tissues, protoderm, ground tissue, and procambial strands accompanies or follows the extension growth of the stem. Procambial strands, which later differentiate as primary xylem and primary phloem tissues (Fig. 1-11B), extend into the newly developing leaf primordia and, within the stem, form an interconnected system of vascular strands.

3.2.2.3. Lateral Bud Initiation

Lateral buds are usually initiated at the flanks of the shoot meristem by localized cell divisions in the axils of leaves (the angle between the leaf and the stem). The lateral bud acquires its own shoot apex and leaf primordia and is a miniature shoot. In herbaceous plants and shrubs, which show abundant branching, it may grow into a branch with expanded leaves soon after its initiation (e.g., two newly initiated buds and two young branches are seen in Fig. 1-11). In plants with a strong dominant main shoot(s), lateral buds close to the main shoot apex stay dormant for a long time; however, if the dominant shoot is cut or injured, they grow out and one of them forms a new dominant shoot. In perennial plants, buds produced near the end of the growth season first produce a few scale leaves followed by a few normal foliage leaves, which stay unexpanded, and with little internodal extension. Scale leaves ensheath and protect the apical meristem and the young leaves until growth resumes (Fig. 1-12).

In many plants, the close association between the site of lateral bud initiation and a leaf described earlier is not evident. Also, in many cases, buds arise at nodes further down in mature parts of stem, probably from progenitor cells derived from shoot meristem that were left in a quiescent state to take up cell division and bud formation activity later.

3.2.2.4. Floral Apex

The transition from vegetative to flowering shoot apex is accompanied by dramatic changes not only in the structure of the apex, but also in patterns of cell division and growth and the nature of derivatives (Fig. 1-13). The tunica-corpus organization of the vegetative shoot meristem is lost and cell divisions spread throughout the apical meristem. Instead of leaves and buds being formed, floral parts—sepals, petals, stamens, and gynoecium (or pistil)—are initiated and there is little elongation growth between initiation of these parts. As a result, the floral parts are borne on a condensed axis, and the flower is a condensed shoot. The shoot (or floral) apex is used up in the formation of the floral parts and its meristematic potential is terminated. Floral parts, like leaves, are determinate organs, and the flower is a determinate shoot.

There is an infinite variation in the structure of flowers: their size, number, and presence or absence of individual floral organs, symmetry, fusion of floral organs with each other and with members of adjacent whorls (organs of a different type), and position of gynoecium (specifically ovary) with respect to other floral organs. These variations are ultimately traceable to the patterns of cell division and growth in the floral apex. Flowers may also be borne in clusters (**inflorescences**). In some inflorescences, such as racemes (e.g., fox glove, *Digitalis purpurea*) and panicles (e.g., oat, *Avena sativa*), the original apex may continue its activity for considerable periods while producing laterals, which terminate in flowers. In others, such as a head (e.g., sunflower, *Helianthus annuus*), the inflorescence axis is condensed and many flowers are borne spirally on the condensed axis.

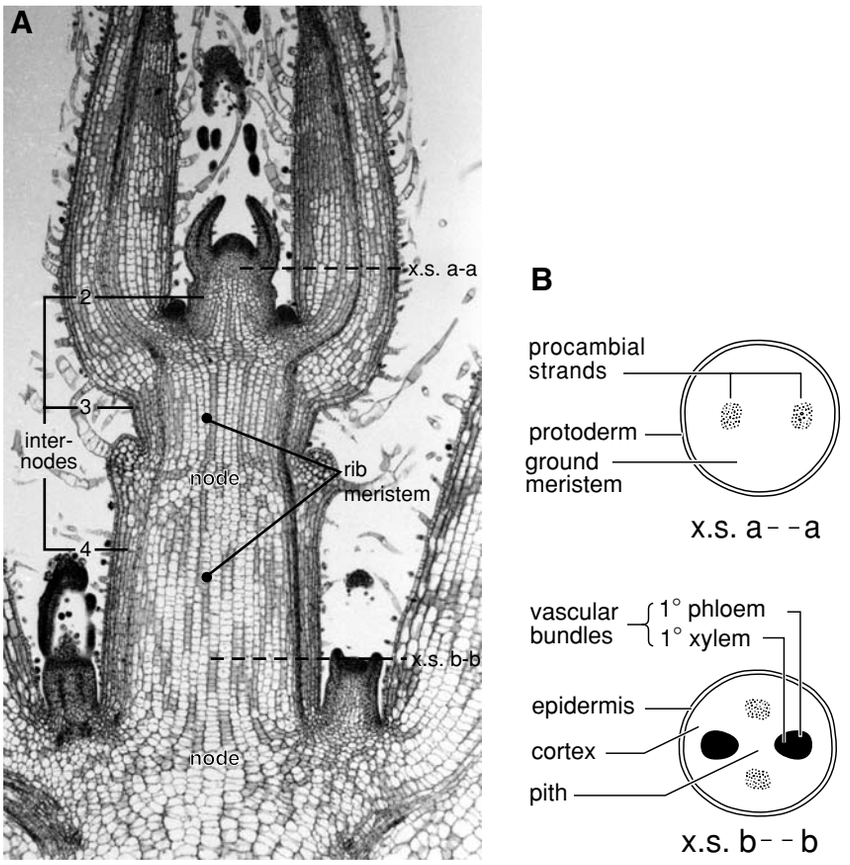
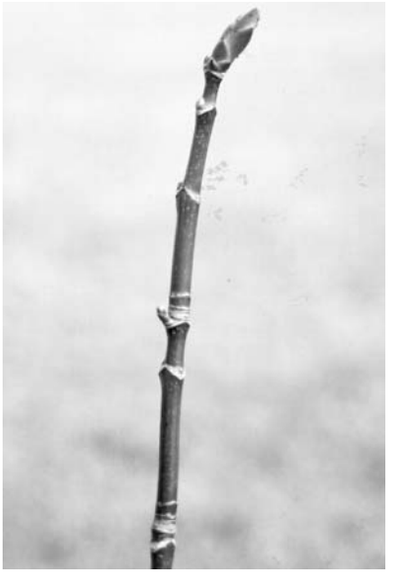


FIGURE 1-11 Extension growth and differentiation of primary tissues in a dicot stem. (A) Rib meristem activity in a *Coleus* stem. Five leaves, including the youngest leaf primordium, and four internodes, appear in this section. Note the longitudinal files of transversely dividing cells, the result of rib meristem activity, in internodes 3 and 4. In older internodes further down, this activity ceases and derivative cells stop elongating with the result that the internodes also cease elongation. Courtesy of Nancy Dengler, University of Toronto, Toronto. (B) Simplified drawings of a dicot stem in cross sections at two levels illustrating the differentiation of primary tissues (x.s. at level a–a) and primary xylem and phloem in procambial strands (x.s. at level b–b).



3.2.3. Secondary Growth and Vascular Cambium

In gymnosperms and woody dicots, a vascular cambium makes its appearance in that region of root or stem that has ceased elongating and produces secondary xylem and phloem. The addition of secondary vascular tissues, especially xylem, adds to the girth of these organs and provides the needed structural support to trees. Small amounts of secondary growth may also occur in some species in petioles and midveins of leaves and in axes that bear flowers, but because these organs have only a limited life span, it is never extensive. Many herbaceous dicots also develop a cambium, but it may

FIGURE 1-12 A terminal and several lateral buds in maple (*Acer saccharum*) at the time of bud break in spring. These buds have a shoot apex and a few scale leaves followed by a few vegetative leaves. There is little internodal elongation. Scale leaves, seen well in the terminal bud, enclose and protect the lateral shoot until it is induced to grow.

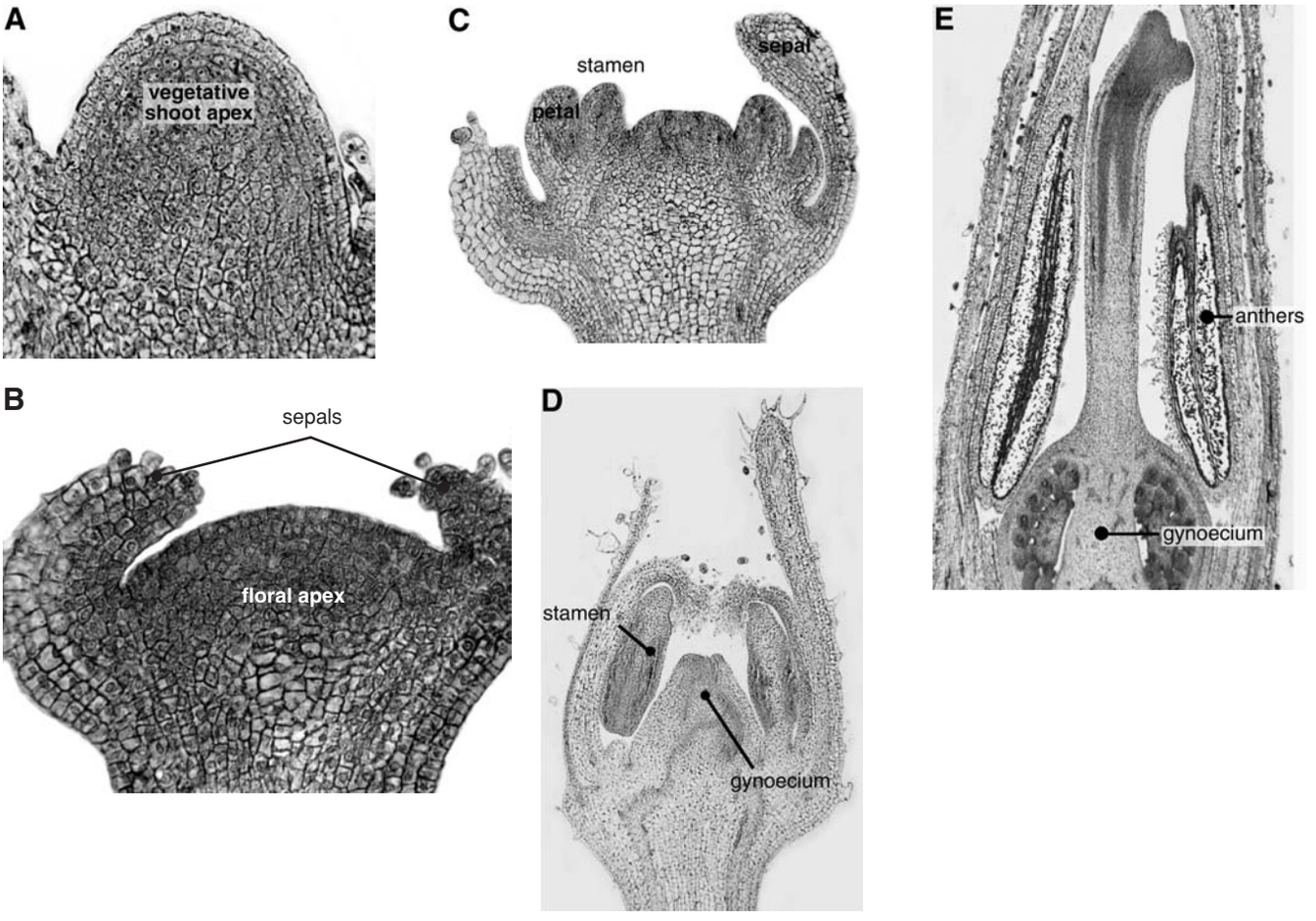


FIGURE 1-13 Longitudinal sections showing the transition from a vegetative to a floral meristem and the development of floral organs in tomato (*Lycopersicon esculentum*). (A) Vegetative shoot meristem. (B) Transition to flowering meristem; sepals have originated. (C) Origin of petals, stamens, and gynoecium. Sepals are in the outermost whorl. (D) Later stage in the development of stamens and gynoecium. (E) Further development and maturation of gynoecium. Anthers, the pollen-bearing structures in stamens, are fully mature. Note that the floral parts develop in a certain order. In tomato, sepals are the first to be formed and mature gynoecium is the last. Photographs are at different magnifications. Courtesy of Vipen Sawhney, University of Saskatchewan, Saskatoon.

not form a complete ring and its activity may be restricted to the vascular bundles.

The vascular cambium is a layer of meristematic cells (or initials) that arises between primary xylem and phloem. Although it is a single layer of cells, in actual practice it is difficult to distinguish that layer from its immediate derivatives on either side. Hence, the term cambial zone is used (Fig. 1-14A). With few exceptions, the cambium consists of two types of initials; the fusiform and ray initials (Fig. 1-14B–D). Fusiform initials are elongated cells that divide periclinally and give rise to axially elongated cells in the xylem and phloem, i.e., is, tracheary cells, sieve elements, fibres, and parenchyma cells or vertical files of parenchyma cells, called parenchyma strands. Ray initials are more or less isodiametric and occur in clusters that appear spindle shaped in tangential sections. Ray initials give rise to xylem and phloem rays, which extend radially into the xylem and phloem and provide for the radial transport of water, minerals, and photoassimlate.

The vascular cambium originates in roots and stems in slightly different locations (for origin in stems, see Fig. 1-1), but eventually in woody plants it forms a complete ring—it extends up and down the stem or root like a cylindrical sheath. How this sheath of cells with two distinct types of initials and a specific spatial arrangement comes to originate in procambial strands has not been studied closely and the details of transition are unknown.

Procambial strands are composed of narrow elongated cells. In dicots and gymnosperms, some of these cells escape differentiation as primary xylem or phloem cells and are left in a potentially meristematic state. Most likely, some of these cells become committed

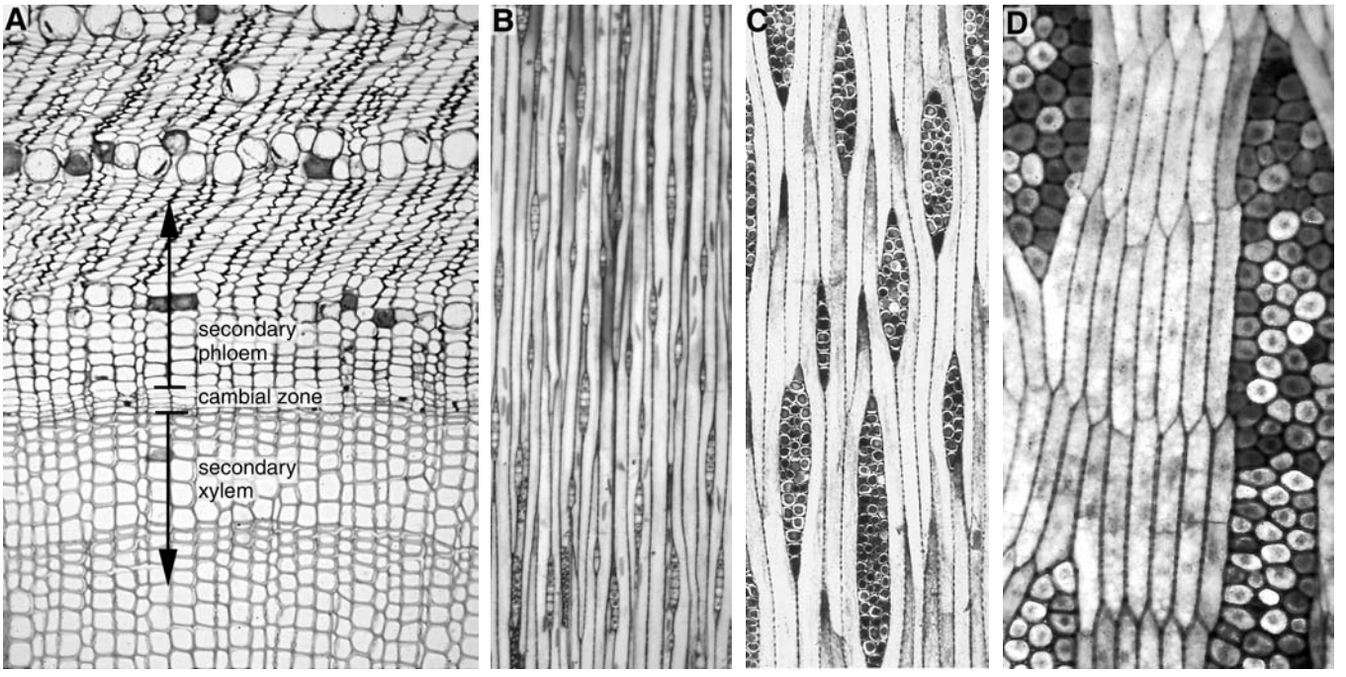


FIGURE 1-14 (A) Cross section of a pine (*Pinus* sp.) stem showing the location of the vascular cambium, secondary xylem, and secondary phloem. Tangential longitudinal sections through cambia of three woody trees, pine (B), birch (*Betula* sp.) (C), and black locust (*Robinia pseudo-acacia*) (D), showing the arrangement and orientation of the fusiform and ray initials. Note that in pine and birch the fusiform initials have ends that overlap with each other, whereas in black locust they are in tiers one upon another. Cambia with the former type of arrangement of fusiform initials are referred to as nonstoried cambia, whereas those with latter type of arrangement are referred to as storied cambia. Also note the differences in the width and the height of rays in the three species. Reproduced with permission from Arnoldia (1973).

as fusiform initials, which, likewise, are elongated cells, whereas others give rise to ray initials after divisions. The actual process is probably more complicated and occurs over some time, but eventually results in the conferment of a new polarity, which is unique to cambium. Cambial cells divide in a strict periclinal plane and give rise to derivatives whose destinies are predetermined as xylem or phloem cells.

Cambium is not, however, a static cell layer placidly cutting out derivatives on each side, which differentiate as xylem and phloem cells; rather it is a seat of constant and dynamic change in interrelationships among fusiform and ray initials. In addition to dividing periclinally, cambial initials also divide periodically in an anticlinal plane (at right angles to the periphery of the stem or root) to add to their numbers and thus cope with the increasing diameter of the wood cylinder, a result of their own activity. In cambia that have been studied in detail, fusiform initials divide anticlinally with much greater frequency than required—far more cells are produced than needed. Excess cells are converted to ray initials by further divisions or they cease dividing and are lost from the cambial ring by differentiating as xylem or phloem cells. As a result, interrelationships among cambial initials are constantly changing and confer upon the cambium an added measure of plasticity. Such plasticity is useful in accommodating pathogens, such as mistletoe, which draw nutrients from host xylem and/or phloem, or in producing more wood on one side to cope with gravity or other environmental stresses, such as snow drifts and leaning boulders.

4. PLANT DEVELOPMENT INVOLVES COMMITMENTS

''Commitment'' or ''determination'' is a general term that includes setting up of polarities and pattern formation. Inherent in the concept of polarity is the presence of poles, typically two, with an axis running between them, thus apical–basal polarity, or in and out (radial) polarity. In contrast, patterning of organs, such as leaf or flower, may show little polarity, but nonetheless are examples of commitment.

The establishment of polarities and patterns during development (e.g., establishment of the root and shoot poles, the distinctive organizations of the root and shoot apices and their respective patterns of growth, the establishment of the vascular cambium and its precise patterns of division and nature of its derivatives) are an intriguing developmental phenomena, which are still only partly understood.

Some of these topics are covered in Chapters 3 and 4. Here it is important to note that commitments occur at different times in plant development. Some are established early in development, e.g., the first division of the zygote; others are established later, e.g., root and shoot poles in the heart-shaped embryo; and still others are established even later, e.g., cambial activity after elongation growth has ceased. Thus, plant development is hierarchical in nature and involves a series of progressive commitments. The second thing to note is that once established, these commitments stay throughout the life of the plant. They confer on the plant a sense of up and down and in and out, what may be considered an apical/basal polarity and a radial polarity. These polarities are essential for an orderly growth of the plant. They are maintained throughout the life of the plant unless perturbations occur in its environment.

There are numerous examples to show commitments and their stability. Two are given here.

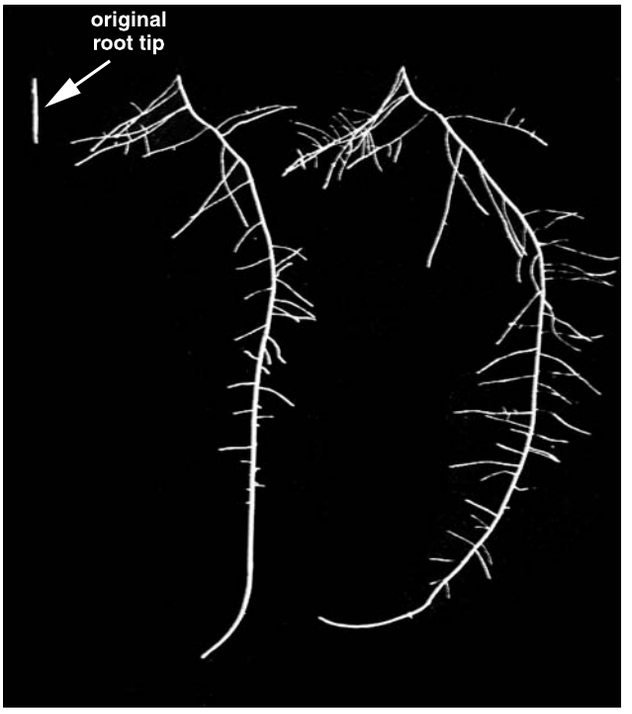


FIGURE 1-15 Root tips in culture. A typical clone, age 355 days, which had been subcultured 23 times, was used as the source for the root tip shown at the upper left; middle figure, 12 days later, and figure on the right, 4 more days later. Slide courtesy of the late Phillip White.

4.1. Determined State of Meristems

The apical root and shoot meristems, and lateral meristems, such as vascular cambium, are unique tissues in that they retain their determined state while continuing to divide and produce derivatives that go on to differentiate as different cell types. Some authors have distinguished between ''proliferative'' and ''formative'' cell divisions. The former allow meristematic cells to perpetuate themselves while retaining their determined state, whereas the latter allow derivative cells to pass to the next stage of determination or differentiation.

A good example of meristems retaining their determined state is provided by root tips in culture. Excised root apices kept in culture continue to grow almost indefinitely, they can be subcultured, but all they produce is root tissue. One such culture started in Jackson Laboratories, Bar Harbour, Maine, in 1927, was still going in 1968 (Fig. 1-15).

Excised shoot apices in culture also produce stem tissues and leaves and, at least in early stages of culture, no roots. Later, because of the production of endogenous hormones, they produce roots as well and form whole plants. These experiments suggest that root and shoot apices, once determined, continue to produce root and shoot tissues, respectively, unless some additional perturbations occur. Appropriate hormonal treatments can provide a further stimulus for roots to produce shoots and for shoots to produce roots.

Similar culture experiments with vascular cambium have been tried, but without success. However, a slightly different type of experiment has been done with vascular cambium. If a square block of tissue, including the cambium, is lifted off a tree trunk (it is possible to do this in the first flush of spring growth when the bark slips—the break occurs in the young xylem cells, not cambium), rotated by 90°, replaced, and some judicious pressure applied on the block, the wound heals in time, and the lifted block continues to produce xylem and phloem cells on the two sides, but the new cells that are produced are elongated horizontally in line with the orientation of the fusiform initials and not vertically as the neighboring fusiform initials and their xylem and phloem derivatives (Fig. 1-16). Some pressure is needed for this orderly continuation of the cambial activity because, in its absence, fusiform initials divide up into numerous small cells and form an unorganized tissue mass, known as the **callus**. The callus may eventually show organization and differentiation, but that is another story.

If a cambial explant is lifted off and put on solid culture medium, it again forms a callus, which may

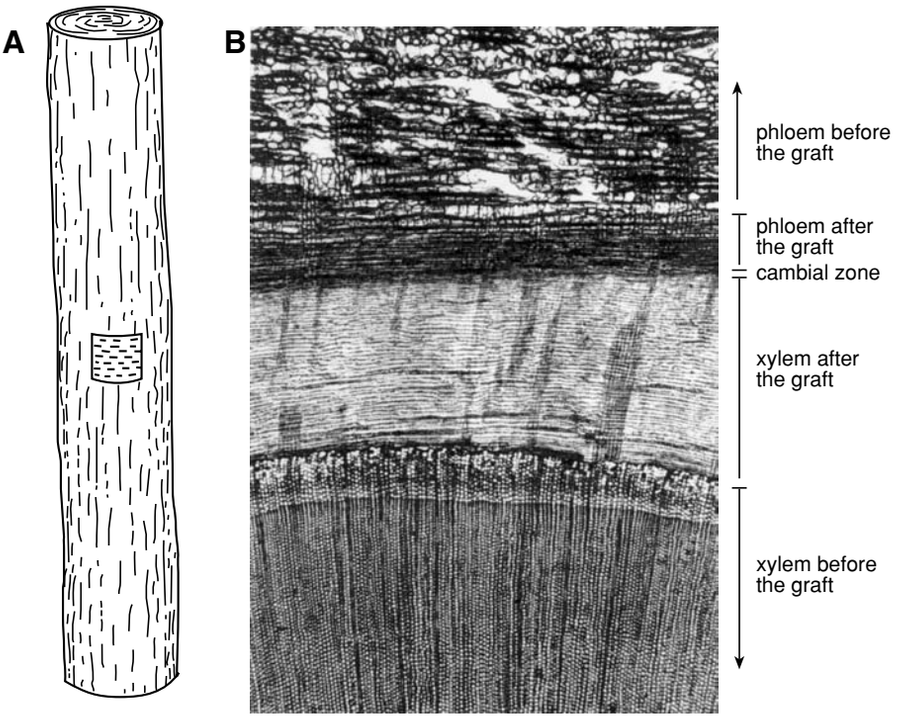


FIGURE 1-16 Determination in vascular cambium. A square block of bark tissue (all tissues external to young differentiating secondary xylem) is lifted off, replaced after being turned by 90°, and some pressure applied (A). The graft takes hold and the new secondary xylem and phloem are produced in line with the changed orientation of the cambial initials at right angles to the previously produced secondary xylem and phloem (B). From Thair and Steeves (1976).

continue to divide, albeit at a slow pace, but lacking the precise orientation of cell divisions as well as the earmarked destiny of the derivative cells, two properties that characterize the cambium.

4.2. Polarity in Shoot and Root Cuttings

A common horticultural practice to propagate plants, especially dicots, is to take stem cuttings and get them to root by putting them in soil or moist air. Adventitious roots are produced at the morphologically basal end of the stem, not the apical end (Fig. 1-17). If the stem segment is inverted, the roots are still produced by the morphologically lower end. Conversely, the shoots are produced at the morphologically upper end. Even though the two cut ends look the same, they are physiologically distinct. Experiments demonstrating this physiological polarity were performed by Julius Sachs more than 100 years ago.

Similar experiments showing physiological polarity can be conducted with cut roots as well, e.g., dandelion roots, where the shoots are produced from the proximal end, that is, the end closer to the root-shoot junction, whereas new roots are produced near the distal end, that is, the end farther away from the root-shoot junction.

5. EXTERNAL OR INTERNAL PERTURBATIONS MAY CAUSE A REVERSAL OF ESTABLISHED COMMITMENTS

The established commitments are not immutable. Plants respond to external or internal perturbations, such as a change in environment, pathogen attack, wounding, hormonal imbalance, in various ways, and in some cases by a reversal of their established commitments. The extent of reversal, whether partial, i.e., going back a few steps, or complete, going back to the zygotic stage, seems to be a function of the extent of perturbation. Two terms, **dedifferentiation** and **redifferentiation**, are used to denote a reversal of established patterns and differentiation along new lines. Cell divisions play important roles in many of these reversions.

The following examples show a reversal of commitments.

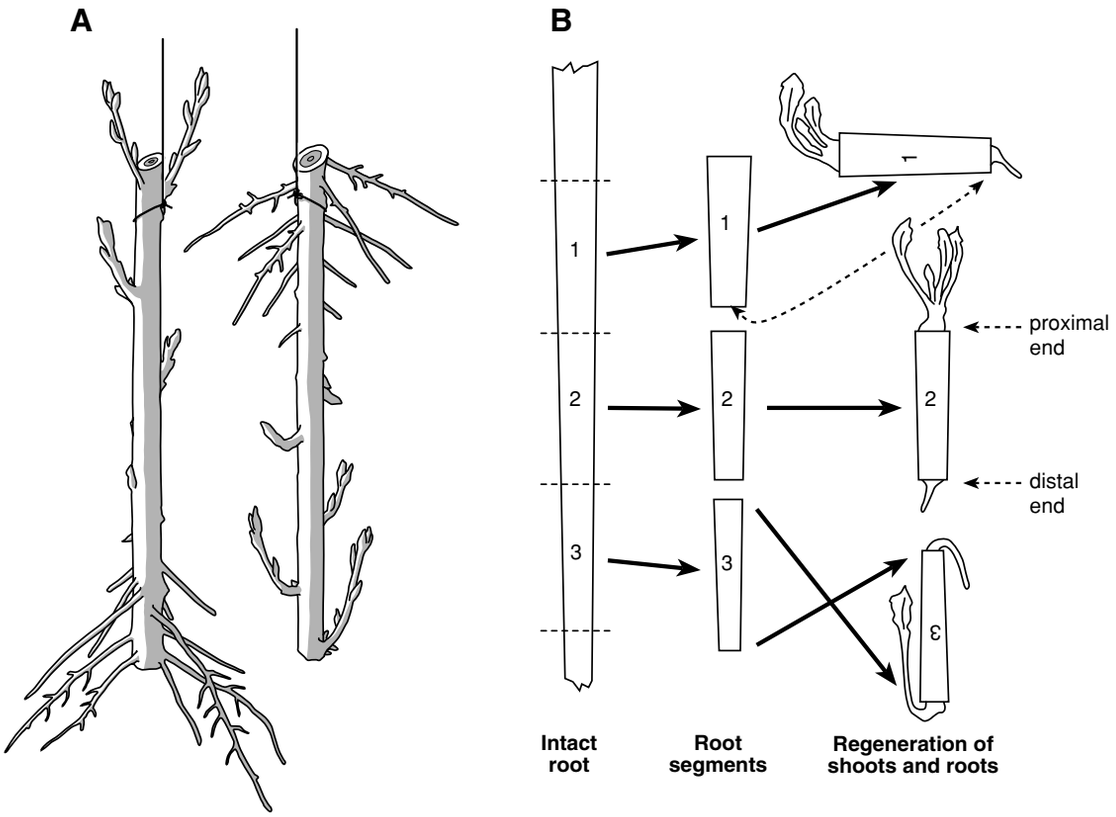


FIGURE 1-17 Polarity in shoots and roots as shown by induction of rooting in cut stems and of shoot buds in cut roots. (A) Stem cuttings of a willow (*Salix*) suspended in moist air in normal and inverted orientations. Roots grow out at the morphologically lower end and shoot buds at the morphologically upper end, regardless of orientation. (B) Roots from plants such as dandelion (*Taraxacum*) or chicory (*Cichorium*) can be segmented and placed in varying orientations. Shoot buds develop at the end originally furthest from the root tip (proximal), and roots develop at the end toward the root tip (distal), regardless of orientation. From Wareing and Phillips (1981) and Warmke and Warmke (1950).

5.1. Production of Whole Plants from Leaf Tips or Margins

Many plants, such as the succulents, *Bryophyllum*, and *Crassula*, Mexican Hat plant, *Begonia*, *Saintpaulia*, reproduce vegetatively by producing small plantlets with leaves, stem, and roots along leaf margins (Fig. 1-18). In time, these plantlets fall off the leaf and establish themselves as new plants. In *Bryophyllum*, groups of cells at leaf margins are left undifferentiated to produce these plantlets; in others, seemingly mature cells at leaf margins or leaf surface resume meristematic activity and the products differentiate into root, stem, and leaf primordia. In the orchid, *Malaxis padulosa*, clusters of small globular embryos are produced at the tip of a mature leaf, which later fall off and grow as new plants. In this case, also, mature cells at the leaf tip resume meristematic activity and form embryo-like structures.

5.2. Production of Adventitious Roots and Shoot Buds

We saw earlier production of roots from stem cuttings and, conversely, production of shoot buds on root cuttings. These things occur naturally as well. Many climbing plants, such as ivy, produce adventitious roots from the stem tissue. These roots produce a sticky material, which is useful in anchoring the plant to the support (wall or a tree trunk). Likewise, many plants, such as poplar, black locust, and redwood, produce shoot buds on their roots—they are called **root sprouters**; in time, shoot buds grow out as new plants far away from the main plant.

In the production of roots from stems, cell divisions occur in parenchyma cells in the vascular region (stem tissues in angiosperms and gymnosperms lack a pericycle) and new rootlets are initiated that break through the stem cortex and dermal tissue (Fig. 1-19). The formation of shoot buds on roots seems to occur in the

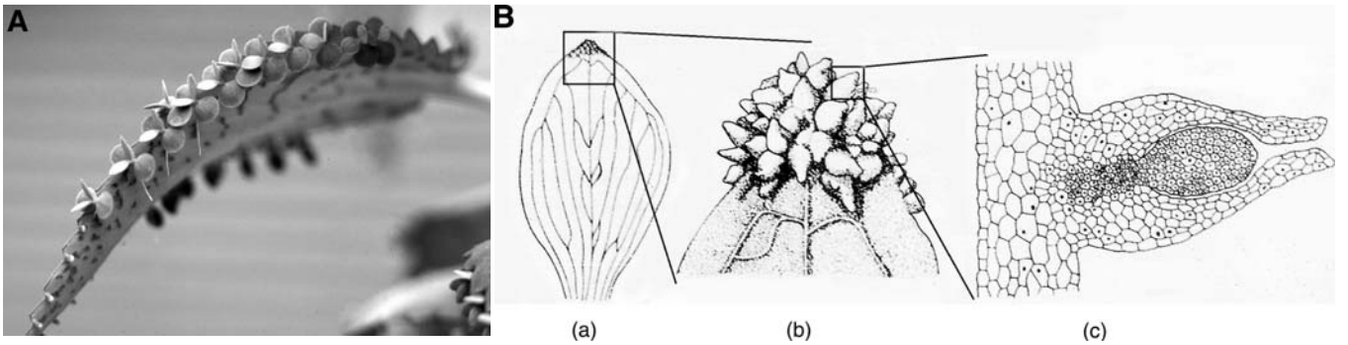


FIGURE 1-18 Production of foliar embryos in the Mexican Hat plant (A) and in *Malaxis padulosa* (B). Demarcated areas in B (a and b) are shown at higher magnifications (b and c, respectively) From Steeves and Sussex (1989).

same manner as that of lateral roots—cell divisions occur in pericycle or vascular parenchyma to produce a group of cells that later gets organized as a shoot bud. In both cases, cells with established destiny undergo partial dedifferentiation followed by redifferentiation along new lines.

5.3. Cells in Culture Can Dedifferentiate Completely

Under certain conditions, complete dedifferentiation can occur. If a cambial explant is put in a liquid culture and shaken gently, fusiform and ray initials lose their precise spatial arrangements and planes of division altogether, they divide in all planes and become similar to ''undifferentiated'' parenchyma cells (Fig. 1-20). They lose their differentiated or determined state and become ordinary parenchyma cells.

This leads us to the well-known phenomenon of regeneration of whole plants from single cells, other than zygote, or **somatic embryogenesis**. In the early-years of the 20th century, Haberlandt had speculated on the potential totipotency of plant cells. Almost 50 years later, and after numerous attempts by different scientists, Steward *et al*. (1957) showed that if explants from carrot roots were put in liquid culture supplied with coconut milk and the flasks were rotated gently, single cells were dislodged from their neighbors and showed asymmetric divisions typical of embryo development. These young ''embryoids'' could be removed from the flask and planted on solid agar to give in time mature carrot plants, which flowered and set seed normally (Fig. 1-21).

This landmark work has been repeated in hundreds of laboratories around the world, with different plants and different sources for the initial inoculum. This

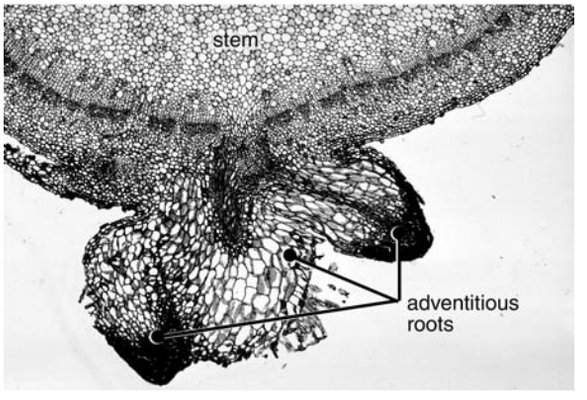


FIGURE 1-19 Production of adventitious roots in stems of climbing ivy (*Hedera helix*). A transverse section of the stem is shown with parts of three adventitious roots.

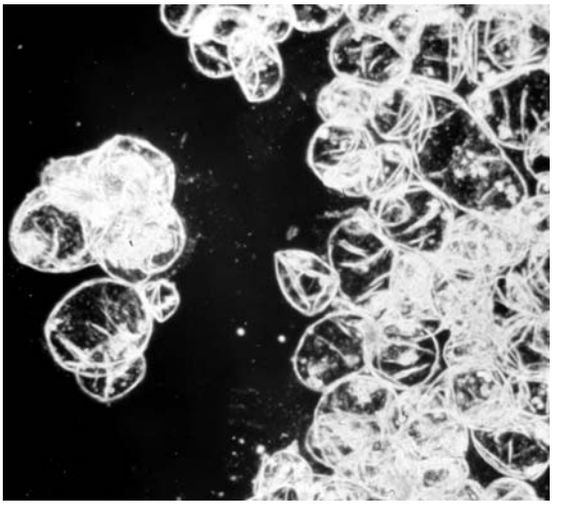


FIGURE 1-20 A cambial explant from sycamore (*Acer pseudoplatanus*) was placed in liquid culture medium and shaken gently. Cambial cells divide in all planes and lose their determined state. Courtesy of Peter Albersheim.

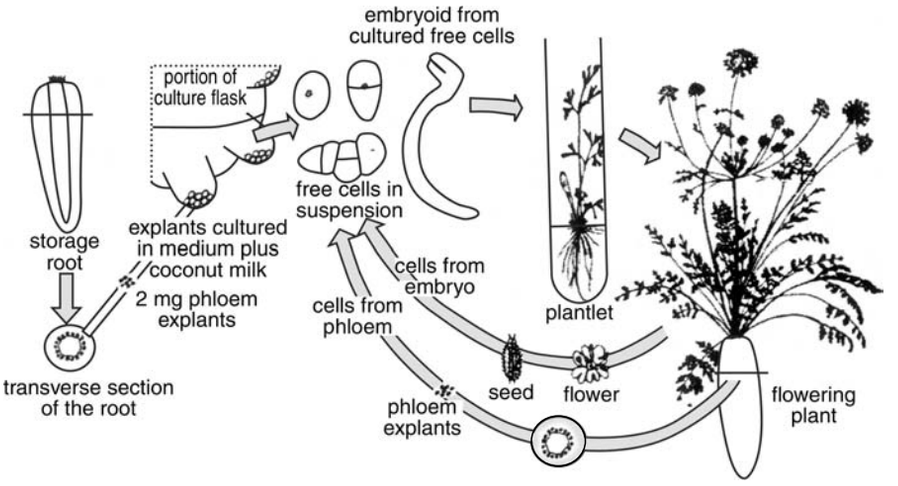


FIGURE 1-21 Production of whole plants from single cells in carrot. From Steward (1968).

capacity of single cells, other than zygote, to produce whole plants, the so-called **totipotency** of plant cells, is covered in Chapter 3. It is a standard tool utilized in the modern-day genetic engineering of plants.

6. CHAPTER SUMMARY

This chapter reviewed the basic aspects of plant embryogenesis and development of the adult body to serve as a backdrop for other chapters in Section I of this book. Plant development is characterized by an open form of growth, which means that it occurs continuously throughout the life of the plant because of the activities of the root and shoot apical meristems and vascular cambium. New, but same, body parts and tissue types are produced iteratively with a possibility for change as environmental factors change with time. Plants also show open differentiation. Body parts, tissues, and cells do become committed, they do differentiate and specialize for a function, but they retain the ability under certain circumstances to turn back the clock, partially or all the way back to the zygotic state, and enter a new developmental program. Chapter 4 considers the phenomena of determination, differentiation, and dedifferentiation. Here it is important to emphasize that both open growth and open differentiation confer upon plants a unique ability to alter their growth patterns depending on changes in their environment. This plasticity of growth is generally not available to most higher animals. These are strategies that plants, being rooted, have evolved to survive on earth.

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