MECHANISMS IN PLANT DEVELOPMENT

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Preface

Developmental biology is the study of how each cell in a multicellular organism acquires and maintains its specialized function. In plants, development is continuous, occurring throughout the life cycle. Multiple factors, both environmental and endogenous, combine to regulate cell specification, generating the enormous diversity of plant forms.

This book is about the mechanisms that regulate plant development. It is structured around these mechanisms and not around the stages of the life cycle, because similar regulatory mechanisms act at different stages of the life cycle and in different parts of the plant. The book is intended for final-year undergraduate courses in plant development and for graduate readers. It is obviously not a comprehensive treatise of all that is known about plant development, but we hope it will provide a conceptual framework from which to build an understanding of the subject.

We would like to thank Francesca and Joshua for going to bed on time every night so that we could write it.

Introduction

The central question of developmental biology is how does a single cell become a complex organism. The initial answer to this question must be descriptive. Reasonably complete cellular-level accounts of development now exist for a number of species, cataloguing the combinations of cell division, cell growth, cell differentiation, cell death and—in animals—cell migration that generate the adult organism. However, whilst a good description is essential, in order to understand development we must understand the mechanisms that control it. What factors control the behaviour of cells, directing them toward division, growth, migration, differentiation or death?

This book discusses the mechanisms underlying the development of flowering plants (the angiosperms). Plant development is not restricted to any one phase of the life cycle, but rather new structures such as leaves, roots and flowers are produced continually. Research aimed at understanding the control of plant development must therefore cover all stages of the plant's life cycle. None the less, similar developmental mechanisms may operate at different stages and consequently this book is not organized around the plant's life cycle, but instead it focuses on the developmental mechanisms themselves.

To put the discussion of mechanism into context, Chapter 1 gives a brief description of angiosperm development. This is intended both as an introduction for those who are unfamiliar with plant development, and as a reference to accompany later chapters. Chapter 2 then considers the implications of key cellular and larger scale characteristics of plant development for the study of development mechanisms.

To produce a functional plant, cells must adopt fates appropriate to their position. Leaf cells must adopt leaf fates; root cells must adopt root fates; cells on the surface of the leaf must behave differently to cells in internal layers; and so on. Chapters 3, 4, 5 and 6 discuss how cell fate is related to the position of the cell in the plant. Chapter 3 considers cell-intrinsic information, such as lineage. Chapters 4, 5 and 6 describe research into the mechanisms that generate cell-extrinsic positional information.

One of the most striking characteristics of plant development is its plasticity in response to environmental cues. This encompasses both spatial aspects of development, such as the direction of growth; and temporal aspects such as the timing of bud growth and the production of flowers. Chapters 7 and 8 discuss developmental responses to environmental information. Chapter 7 considers the many developmental effects of light. Chapter 8 outlines research into responses to other environmental cues. The effects of internal and

environmental information on development are closely coordinated. Chapter 9 discusses this topic in relation to the development of the shoot.

Last of all, Chapter 10 compares the mechanisms that control plant development with those that operate in animals.

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CHAPTER 1

An introduction to flowering plants

The angiosperm life cycle alternates between an extensive **diploid phase** and a more restricted **haploid phase**. The diploid phase is what we recognize as a plant. Its development consists of: (i) **embryogenesis**; (ii) **germination**; (iii) **primary development**, in which shoots and roots elongate and branch; and (iv) **secondary development**, in which shoots and roots thicken. Overlapping primary and secondary development, plant development may be **vegetative** or **reproductive**. Vegetative development is divided further into a **juvenile phase** and an **adult phase**.

Alternation of generations

The names of the haploid and diploid phases of the plant's life cycle reflect the type of reproductive cells that each produces. The haploid phase of the plant is called the **gametophyte** because it produces male and female **gametes** by mitosis. These fuse to form the **zygote** from which the diploid phase develops. Likewise, the diploid phase of the plant is called the **sporophyte** because it produces haploid **spores** by meiosis, from which the haploid phase of the plant develops. In flowering plants there are separate male and female gametophytes, producing sperm and egg cells, respectively. The female gametophyte develops from a **megaspore** and the male gametophyte forms from a **microspore**. Both gametophytes consist of only a few cells that are entirely dependent on the sporophyte for their nutrition.

Gametophyte development

The female gametophyte, which is also called the **embryo sac**, develops within the **carpel** (Fig. 1.1). Carpels typically consist of an **ovary**, a filament called the **style** and a sticky receptacle called the **stigma**. The ovary

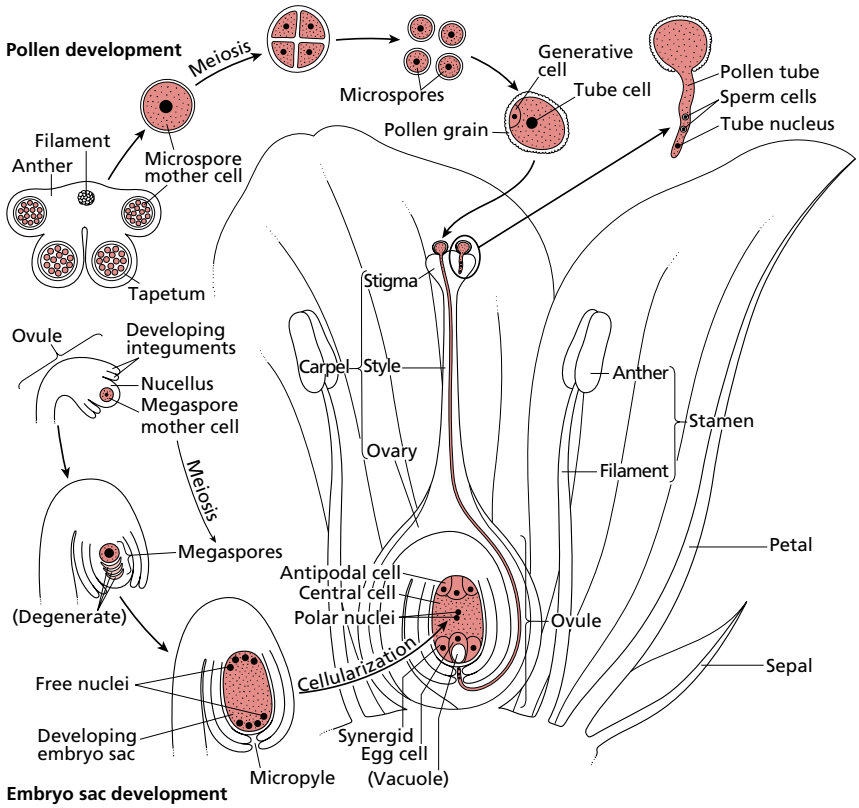

Fig. 1.1 Gametophyte development in angiosperms. The female gametophyte develops in the ovule and forms the embryo sac. The male gametophyte develops in the anther and forms the pollen grain.

holds one or more ovules and these are the sites of embryo sac development. Each ovule contains a roughly egg-shaped mass of cells called the **nucellus** and surrounding this there are two outer layers of cells called the **integuments**. The integuments do not quite join at the tip of the ovule but leave a small gap called the **micropyle**. The development of the female gametophyte begins with the meiosis of a single cell in the nucellus just below the micropyle to create a strand of four haploid megaspores.

In most plants, three of the megaspores degenerate but the fourth, the one farthest from the micropyle, enlarges and undergoes three rounds of mitosis to create an embryo sac containing eight haploid nuclei distributed among seven cells. Three of the seven cells cluster around the end of the embryo sac closest to the micropyle. The cell in the middle of these three is the **egg cell** and the two cells flanking it are called **synergids**. At the other end of the embryo sac there is a group of three cells called the **antipodal cells**, and in the middle of the sac there is a single, binucleate **central cell**. The central cell's two nuclei are called the **polar nuclei**.

Male gametophytes develop in the **anther** at the top of the stamen. Here there are typically four pollen sacs, each of which contains a column of

diploid **microspore mother cells** surrounded by a nutritive tissue called the **tapetum**. Each mother cell undergoes meiosis to form four haploid microspores and each of these develops into a pollen grain. Within the pollen grain, the microspore divides mitotically to produce a **tube cell** and a **generative cell**. In some species, the generative cell immediately divides again to give a pair of **sperm cells**. In most flowering plants, however, this division takes place later, in the tube that develops when a pollen grain germinates.

For fertilization to occur, the pollen grain must germinate on a compatible stigma. The pollen tube grows into the stigma, through the style to the ovary, and enters the ovule, normally through the micropyle. As the tube grows, the tube cell nucleus stays near to the tip and the two sperm cells follow behind. When the pollen tube reaches the embryo sac, it penetrates one of the synergids and then releases both sperm cells. When, or even before, this happens the synergids degenerate allowing the sperm cells access to both the egg cell and the central cell. One of the distinguishing features of angiosperms is that they have double fertilization. One sperm cell fuses with the egg cell to produce the zygote. The other sperm cell fuses with the two polar nuclei in the central cell to create a triploid nucleus from which the **endosperm** (a nutritive tissue) develops.

After fertilization has occurred, the remaining haploid cells of the embryo sac degenerate. Most parts of the parent flower also wither, with the exception of the ovaries which normally develop into the fruit. As the embryo grows, it destroys most of the nucellus. The two integuments, however, normally remain to form the coat of the new seed.

Development of the sporophyte

Embryogenesis

In most species, the zygote divides in a plane perpendicular to the long axis of the embryo sac to produce a large **basal cell** near to the micropyle, and a small **terminal cell** close to what was the central cell and is now the developing triploid endosperm (Fig. 1.2). Subsequent patterns of cell division are more variable, sometimes even within a species, but the appearance of the main tissues and organs of the embryo follows a predictable sequence. The first distinction to arise is between cells that will form the main body of the embryo and those that will produce the **suspensor**, a filament that connects the embryo to maternal tissue near the micropyle. It is always cells at the micropyle end of the embryo that form the suspensor, and cells nearer the centre of the embryo sac that develop into the embryo proper.

Embryos undergo a regular series of changes in shape. During early development, cell divisions occur with little or no increase in the embryo's total size, resulting in a ball of cells called the **globular embryo**. At this stage, different tissues appear. The outermost layer of cells forms an **epidermis** in which the cells are typically smaller than the cells in the underlying tissue. The epidermis of the embryo and the epidermis of immature regions

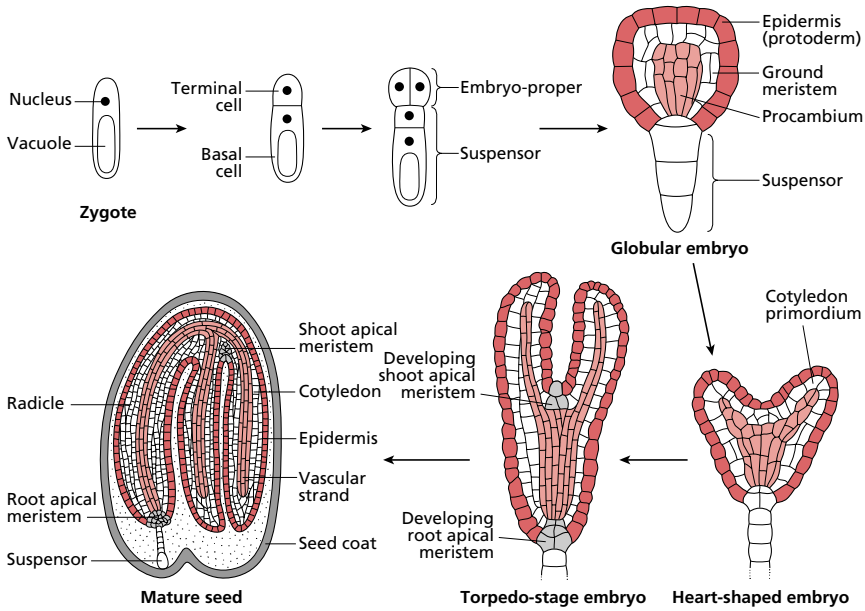

Fig. 1.2 Embryogenesis in *Arabidopsis thaliana*. The *Arabidopsis* embryo develops very rapidly. In many angiosperms each stage of embryo development is longer, resulting in larger embryos consisting of more cells.

of growing shoots and roots are sometimes called the **protoderm**. Deeper in the globular embryo, a distinction appears between relatively large cells with abundant vacuoles and a strand of smaller, less vacuolated cells. This strand will develop into **vascular tissue** and, in this immature state, it is called the **procambium**. The larger cells will form the **ground tissue** of the embryo and, in their immature state, they are sometimes called the **ground meristem**. The precursors of the root and shoot **apical meristems** appear at this stage, or later, as clusters of densely cytoplasmic cells at either end of the procambial strand. All post-embryonic cell lineages originate in the apical meristems. The root apical meristem forms at the end of the procambial strand nearest to the suspensor (and often incorporates the suspensor cell closest to the embryo proper). The shoot apical meristem develops away from the suspensor at the other end of the procambium.

The globular stage of embryo development ends when either one or two **cotyledons** begin to form near the site of the shoot apical meristem. In dicots, two cotyledons develop and the embryo changes from a globular embryo to a **heart-shaped embryo**, with the cotyledons as the two bulges at the top of the heart. The heart-shaped embryo elongates to form the **torpedo-stage embryo** while retaining the same pattern of tissues and organs. Monocots, of course, do not have a heart-shaped stage because they only form a single cotyledon. Depending on the relative sizes of the embryo and the seed, the embryo may fold over as it elongates.

The growth of most angiosperms pauses between the end of embryogenesis and the beginning of germination, but the extent of embryo development

prior to this pause varies between species. In embryos with the most limited development, a shoot apical meristem and a root apical meristem form but immediately become dormant. In other species, some growth occurs at both apical meristems before dormancy: the shoot apical meristem initiates leaves to form the **plumule** and the root apical meristem initiates a short length of root called the **radicle**. In grasses, protective sheaths called the **coleoptile** and the **coleorhiza** enclose the plumule and the radicle, respectively.

Germination

Germination requires the correct combination of external cues such as moisture, temperature and light. During germination, extensive cell elongation forces the root out of the seed case and carries the shoot upwards. The exact anatomy of a seedling depends on the location of cell elongation in the shoot. There are two main possibilities and they are simplest to visualize for a dicot seedling (Fig. 1.3). If elongation takes place between the cotyledons and the radicle (in the **hypocotyl**), the cotyledons are lifted above ground

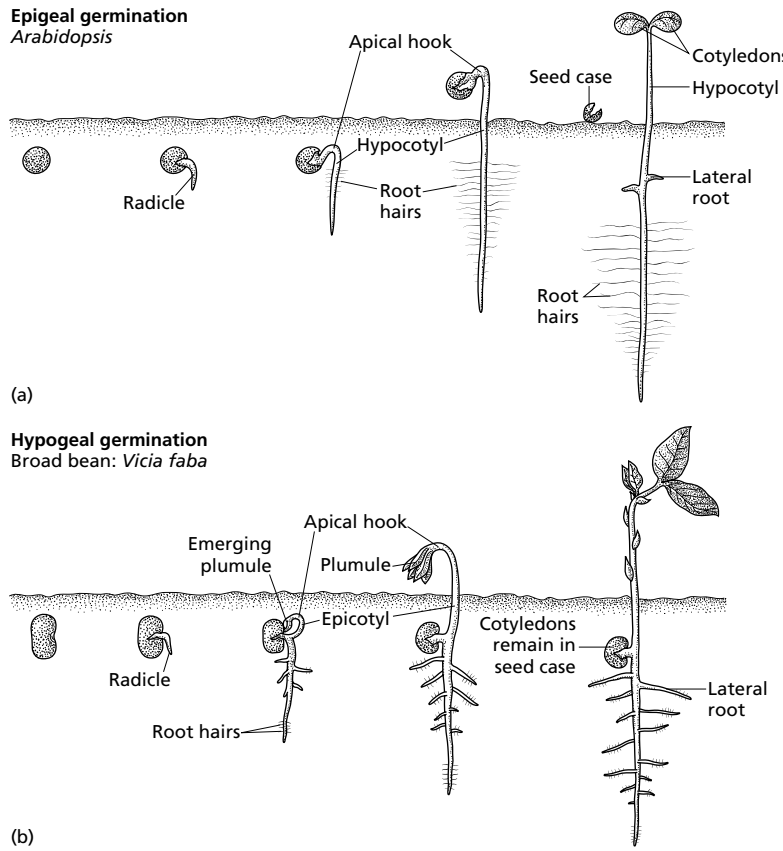

Fig. 1.3 Germination in (a) *Arabidopsis* and (b) the broad bean (*Vicia faba*) (not drawn to scale).

and the seedling is called **epigeal**, meaning 'above the ground'. If elongation takes place between the cotyledons and the shoot apical meristem (in the **epicotyl**), the cotyledons remain underground and the seedling is called **hypogeal**, meaning 'below the ground'. In either case, the germinating shoot grows upwards in a hook shape so that it pulls rather than pushes the shoot tip through the soil. Once above the soil and in the light the hook straightens out, and the cotyledons or leaves of the plumule green up and expand.

Primary vegetative development

The primary development of the plant is that in which shoots and roots lengthen and branch. Shoots and roots elongate due to cell division and cell elongation in and immediately behind their apical meristems. Branching occurs by the development of additional, laterally placed meristems that become the apical meristems of the lateral shoots and roots. Figure 1.4 shows the structures produced during primary development.

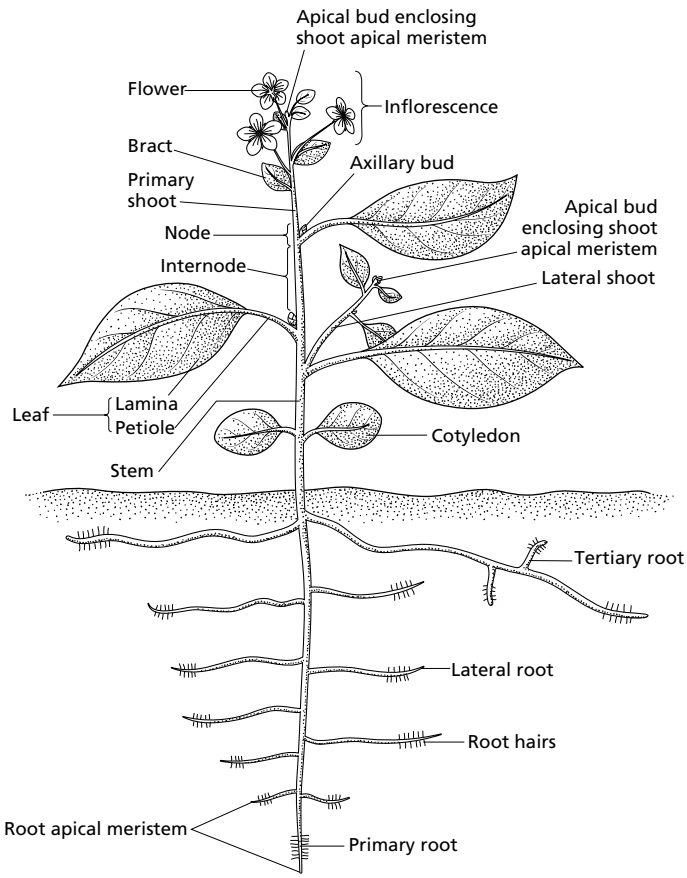

Fig. 1.4 Structures produced during primary development.

Primary development of roots

Root apical meristem

The root apical meristem (RAM) is not at the very tip of the root, but lies behind a protective shield called the **root cap** (Fig. 1.5). Cell divisions in the most apical layers of the meristem add cells to the root cap, replacing those worn away by friction between the growing root and the soil. Cell divisions deeper in the meristem contribute cells to the main tissues of the root. From the circumference inwards, these are the **epidermis**, the **cortex**, the **endodermis**, the **pericycle** and a central core of **vascular tissue**.

When the root is initiated, all cells in the apical meristem normally divide at about the same rate. In many species, however, cells in the centre of the meristem become inactive over time, forming a so-called **quiescent centre**. Cells in the quiescent centre do not lose the ability to divide rapidly but can be activated after damage to the apical meristem. In some plants, the quiescent centre also appears and disappears on a seasonal basis.

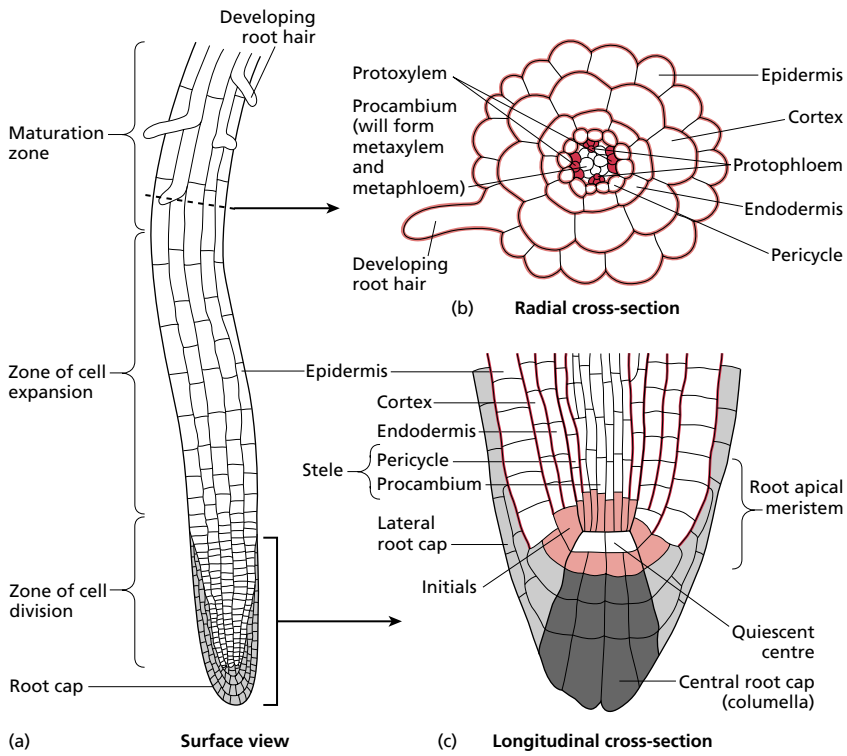

Fig. 1.5 The *Arabidopsis* root. (a) Surface view: a section of root cap has been omitted to show the epidermis down to the level of the root apical meristem. In intact roots, the root cap forms a complete cone around the root tip. (b) Radial cross-section through the maturation zone. (c) Longitudinal cross-section through the root tip.

Development of root tissues

The developing root consists of three relatively distinct zones (Fig. 1.5). At the apex there is a **zone of cell division**. This includes the apical meristem and extends for up to 1 mm into the developing root tissues. Behind the zone of cell division there is a fairly distinct **zone of cell expansion** in which division has virtually ceased. Finally, behind this, there is a **maturation zone** in which the final stages of cell differentiation take place. The exact positions of these three zones can vary between species, growth conditions and tissue layers.

The development of the epidermis consists of relatively uniform cell division and then cell expansion near to the root tip. Following this, a subset of cells differentiate into **root hairs** in the maturation zone.

Beneath the epidermis, one or more layers of **parenchyma** make up the cortex (parenchyma is a general term used to describe tissues consisting of thin-walled, morphologically undifferentiated cells). Inside the cortex, there is a single layer of endodermis. Endodermal cells lay down a band of cork in the cell walls that are oriented at right angles to the surface of the root. This band, called the **Casparian strip**, blocks the passage of water through the walls of endodermal cells. As a consequence, water and minerals absorbed from the soil must pass through the cytoplasm of the endodermal cells before reaching the vascular tissue. This allows the endodermal cells to regulate the passage of solutes into the vascular system and up into the shoot. In the majority of angiosperms the outermost layer of the cortex, called the **exodermis**, also develops a Casparian strip in older non-absorbing parts of the root, where it apparently acts to reduce water loss.

At the centre of the root tip, the root meristem contributes cells to the procambium from which a core of vascular tissue develops, called the **stele**. In most plants, a single bundle of **xylem** forms in the middle of the stele. The bundle of xylem consists of a central region of large-vesselled **metaxylem**, from which arms, or 'poles', of small-vesselled **protoxylem** project. Bundles of **phloem** (which begin to differentiate before the xylem) lie between the protoxylem poles. In each bundle, small-vesselled **protophloem** develops near the edge of the stele, and large-vesselled **metaphloem** develops close to the central xylem. Surrounding both the xylem and the phloem, the stele contains a single layer of parenchyma cells called the **pericycle**.

Root branching

Lateral roots develop in the region behind the band of root hair differentiation. Lateral roots are initiated by a renewal of cell division in the pericycle, normally involving pericycle cells close to one of the protoxylem poles. The developing lateral root grows out through the cortex and epidermis of the parent root to reach the soil. In many plants, cells in the endodermis of the parent root also divide so that lateral roots remain sheathed by endodermis until they break through the parental epidermis.

In some species, roots also produce adventitious shoot buds. These form from shoot apical meristems that usually develop within the pericycle or the

cortex of the root. In some trees, shoot buds may form from tissues in the outer bark of a root following secondary thickening.

Primary development of shoots

Shoot apical meristem

Shoots consist of leaf-bearing **nodes** separated by leafless **internodes** (Fig. 1.4). The shoot apical meristem (SAM) is at the very tip of the shoot and is usually considered to consist of the cells above the youngest **leaf primordium**. Seen from above, most SAMs are circular in outline. Seen from the side, they may be convex, flat or concave.

The SAM has both radial and vertical structure (Fig. 1.6). Considering radial structure, the meristem typically possesses: (i) a **central zone**, which consists of large, slowly dividing cells; and (ii) a **peripheral zone**, in which cells divide more rapidly and are usually smaller. The peripheral zone initiates leaves, axillary buds and the outer layers of the stem. Considering vertical

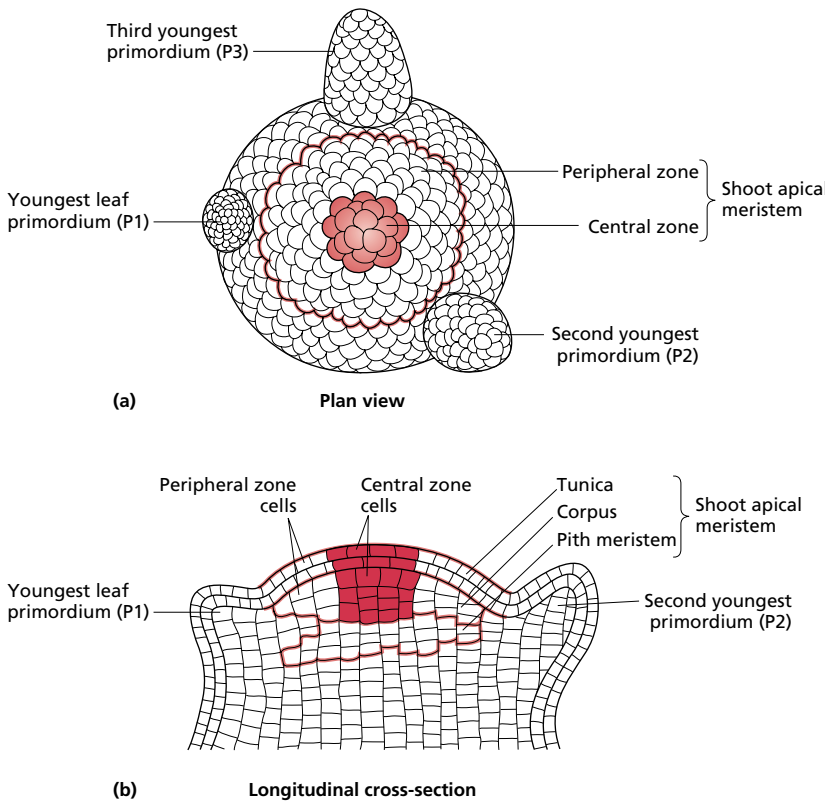

Fig. 1.6 A stylized representation of a dicot shoot tip: (a) plan view and (b) longitudinal cross-section. In most dicots, the shoot apical meristem and young leaf primordia are enclosed by developing older leaves to form the apical bud.

structure, at the meristem surface there are one or more distinct cell layers, collectively called the **tunica**, whereas cells in deeper regions of the meristem are more randomly positioned, forming the **corpus**. The radial and vertical structures of the meristem overlap such that the peripheral and central zones each contain cells from both the tunica and corpus.

In dicots, there is a further group of rapidly dividing cells beneath the central zone that represent the **pith meristem**. These give rise only to the pith of the stem. In monocots, which rarely have a well-defined, central pith (see the description of internode development below), the central tissues of the stem are produced by a large meristematic zone below the apical meristem. This is called the **primary thickening meristem** and can extend both across the diameter of the shoot and for some way down its sides, producing tissue that makes the monocot stem both longer and thicker.

Nodes

Nodes are the sites of leaves and axillary buds. A glance at almost any shoot will show leaves arranged in a regular pattern called the **phyllotaxy**. In some plants, leaves grow as pairs or in groups at each node, but the most common phyllotaxy is a spiral with a single leaf at each node.

Leaves The leaves of dicots and monocots develop somewhat differently and even within each group there is wide variation. Tobacco provides a good example of the basic pattern of dicot leaf development (Fig. 1.7), and the growth of the maize leaf illustrates leaf development in monocots (Fig. 1.8).

Because the absolute rate of leaf growth varies widely with environmental conditions, it is conventional to describe the time course of leaf development in units called **plastochrons**. A plastochron is the period between the initiation of two successive nodes on the shoot. The first plastochron of leaf development in tobacco produces a swelling called a **foliar buttress** in the peripheral zone of the meristem. Normally, the foliar buttress is referred to simply as P1, indicating that it is the youngest visible leaf primordium. The second youngest leaf primordium is P2, and so on. Over the next two plastochrons, the primordium elongates to become peg-shaped. When the leaf is between three and four plastochrons old, the leaf blade (the **lamina**) appears as two bulges flanking the upper face of the primordium, i.e. the face nearest the centre of the apical meristem (the **adaxial** face).

The tobacco leaf develops due to cell division and cell expansion throughout the primordium. The pattern of development is complex with localized, short-lived increases in the division rate in different parts of the leaf lamina. Overlapping these local variations, however, there is a more general pattern. As the leaf matures, cell divisions cease at the tip of the leaf first, and then in a wave moving down to the base of the petiole. The final stages of cell expansion and differentiation occur after cell division stops in each region.

Under sunny conditions, the leaf blade consists of clearly stratified cell types. There is an **upper (adaxial) epidermis**, a **mesophyll** that consists of an upper layer of **palisade parenchyma** and a lower layer of **spongy**

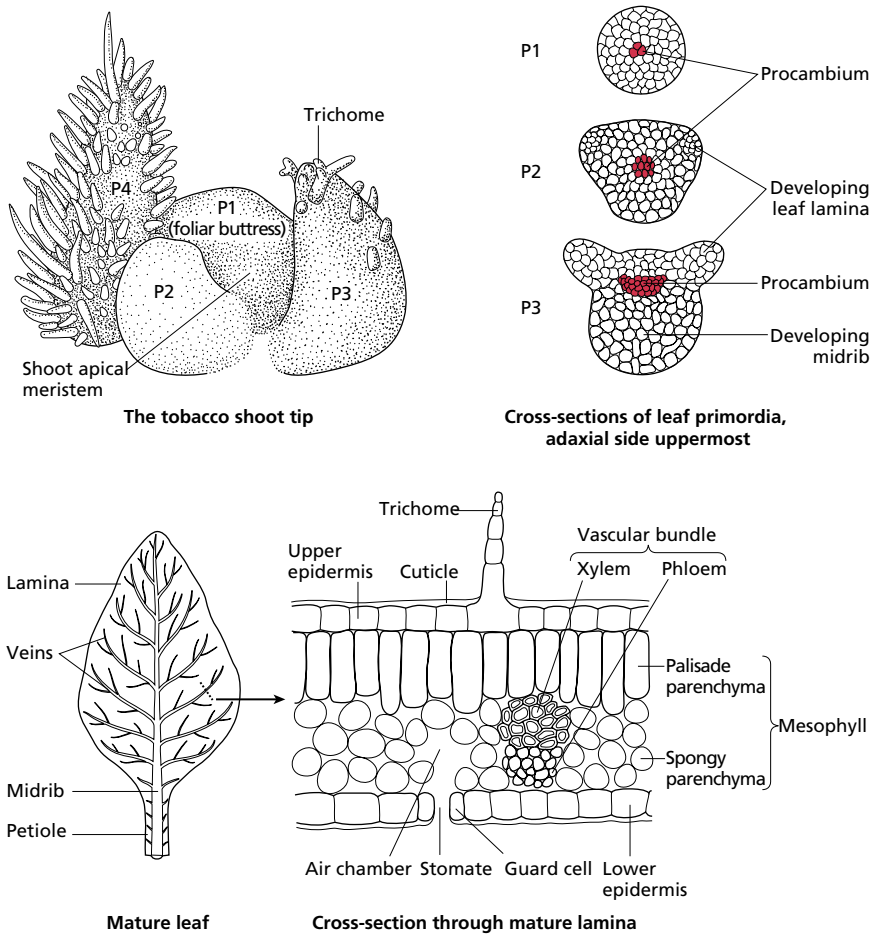

Fig. 1.7 Leaf development in tobacco.

parenchyma (these terms are often simplified to the 'palisade layer' and 'spongy mesophyll', respectively), and then a **lower (abaxial) epidermis.** The epidermis contains **guard cells** around **stomata**, relatively unspecialized **ground tissue** and hairs (**trichomes**, a term used for a variety of epidermal outgrowths including spines, bladders, scales and glands). The mature leaf also has extensive vascular tissue, both in the midrib and as a network of veins in the blade.

The best-studied monocot leaf is that of maize (Fig. 1.8). The maize leaf has two distinct regions. The top of the leaf forms the **blade**, while the base of the leaf wraps around the maize stalk to form the **sheath**. The junction between blade and sheath is clearly marked by two wedges of tissue called **auricles**, and by a flap on the adaxial side called the **ligule**.

The development of the maize leaf begins with the appearance of a primordium that encircles the apical meristem in an overlapping, 'key-ring' shape. A strand of procambium running into the primordium marks the site

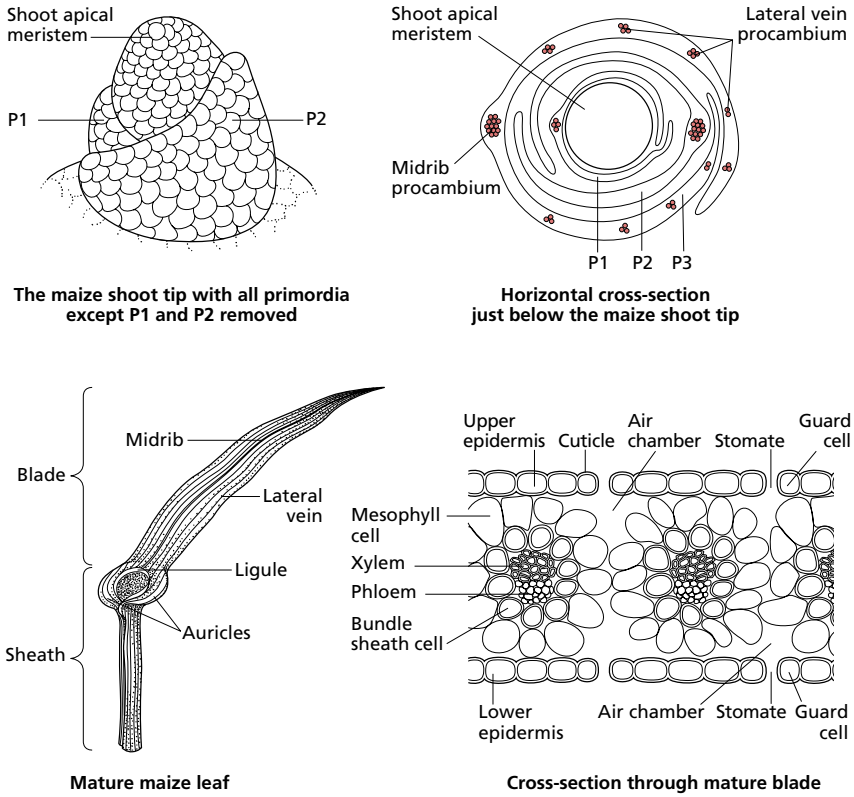

Fig. 1.8 Leaf development in maize.

of the future midrib. By the time the primordium is three to four plastochrons old the **lateral veins** (which run up the maize leaf parallel to the midrib) have been initiated, the region that will form the ligule and the auricles is visible, and the cell divisions that will create the ligule are beginning.

Early in maize leaf development, cell divisions take place throughout the primordium. Later, following the same pattern as the tobacco leaf, cell divisions end in a basipetal wave that begins at the leaf tip and moves progressively towards the leaf base. Although cell divisions have ended in the tip of the leaf by the time the primordium is about 3 cm long, the tip region continues to grow extensively by cell expansion before the final stages of cell differentiation occur. Similar waves of expansion and differentiation follow the cessation of cell divisions down the leaf. As a result, the development of the blade finishes before the development of the sheath. The pattern is so marked that there is a period in the leaf's development when the blade is fully mature but cells are still dividing at the base of the sheath.

The epidermis of the maize leaf contains regular arrays of stomata and ground cells, and may also produce leaf hairs. The pattern of cells in the epidermis is related to the position of veins beneath, for example rows of stomata run up the leaf blade but are never directly over a leaf vein. On the inside, the maize leaf has a specialized internal structure called **Kranz**