

CHAPTER

1

*Development in
the vascular plants*

The vascular plant, like all sexually reproducing organisms, begins its existence as a single cell, the fertilized egg or zygote. Proliferation of this cell leads to the formation of an embryo within which, at an early stage, organs and tissues begin to be formed. Early in embryogeny two distinctive regions are set apart, approximately at opposite poles, that subsequently retain the capacity for continued growth. One of these, designated the *shoot apical meristem*, functions to produce an expanding shoot system by the continued formation of tissues and the initiation of a succession of leaf and bud primordia. The other, the *root apical meristem*, similarly forms an expanding root system. Furthermore, the development of these open-ended systems is repetitive; the same kinds of tissues and organs are produced in continuing succession.

The activity of the apical meristems results in the production of a continuously elongating body, which has been called the *primary body* of the plant. In many cases this primary body constitutes the whole plant. In other cases, particularly in those plants with an extended life-span, there is an additional component of development that leads to an increase in girth of the axis. This results from the activity of two additional meristems that are initiated in the postembryonic stage: the *vascular cambium*, which contributes additional cells to the conducting system, and the *cork cambium*, which produces a protective tissue replacing the original epidermis. These meristems and the tissues they produce constitute what is designated the *secondary body* of the plant. The secondary body does not constitute an entire plant in that it is composed of a few tissue types only and includes no organs. In some cases, however, it comes to constitute the bulk of the plant body.

There is a distinct difference between this pattern of development and that which characterizes the higher animals. In the animal embryo the fundamental plan of the adult body is laid down so that all the organs and tissues are present at least in rudimentary form. Postembryonic development of the animal consists of the enlargement of the body and then its maintenance in a functionally efficient state. Thus, whereas higher animals have characteristic numbers of organs, the indeterminate shoot

has an indefinite number of leaves. On the other hand, this contrast in development between plants and animals should not be overemphasized. There are in the animal body many groups of cells that continue to proliferate throughout the life of the organism, giving rise to such structures as skin, blood, hair, claws, and various epithelial layers. Proliferating cell groups of this sort are very similar to the secondary plant meristems, but there is less similarity to the apical meristems. In these there is clearly a greater developmental potential in that they give rise to a wider range of structures and to a higher level of organization. In fact, they produce the organized plant body. Thus, the differences between plant and animal development are significant, but fundamental similarities should be recognized.

The possible significance of the plant mode of development may be appreciated by considering the cellular structure of plants and their overall immobility. Plant cells are surrounded by a relatively rigid wall and are tightly cemented together within the framework of the tissues. In the animal body, cell replacement, which seems to be essential for the maintenance of functional efficiency of at least certain tissues, can be accomplished within the histological framework. In the plant this obviously is impossible, and a comparable replacement is effected by the continual addition of new cells at the growing tips of shoots and roots by the primary meristems and laterally by the secondary meristems. In a very real sense, plants assimilate at their most recently formed tips. The absorption of water and mineral salts is accomplished at or near growing root tips, and shoot apical meristems continually replenish the complement of photosynthetic leaves, which are shed often after one growing season and at most after several years. These expanding tips are connected by a vascular conducting system that may be renewed by cells derived from the vascular cambium. Moreover, continued growth endows the immobile plant with a measure of responsiveness to its environment, which is seen in the tropistic movements of the plant organs and in the continued advance of roots into unoccupied regions of the soil. It could be argued that, to a limited extent, development plays a role in plant survival analogous to that of behavior in animals.

In the preceding paragraphs we have been using the word *development* rather freely without stating precisely what we mean by it. Certainly, before plunging into the subject matter of this book about development, we have an obligation to state what we intend to encompass under this heading.

Development is the sum total of events that contribute to the progressive elaboration of the body of an organism. A more restrictive definition might unfortunately eliminate from consideration some essential

aspects of the development process. On the other hand, a broad interpretation, such as we have given, might seem to include all or most of the physiological processes of living organisms. This is especially true in plants, in which, in a very real sense, all physiological phenomena throughout the life of the organism seem to be channeled into the progressive elaboration of its body. One might justifiably ask, then, whether such phenomena as photosynthesis or the absorption of water are to be regarded as part of development. Certainly, their absence would preclude development; but they are far removed from the actual mechanism by which the plant body is elaborated.

In order to avoid the impossible requirement of discussing the entire biology of plants, it will be necessary to concentrate upon those phenomena that directly participate in the formation of the plant body. Even in this limited sense, development encompasses numerous processes, such as cell division, cell enlargement, protein synthesis, the elaboration of cell wall materials, quantitative and qualitative alterations in cell organelles, among many others. It is, however, convenient to recognize two major aspects of development and to analyze developmental processes in terms of these two categories. These are growth and differentiation.

In an organism *growth* is an irreversible increase in size, and it is accomplished by a combination of cell division and cell enlargement. Cell division does not of itself constitute growth and in fact may occur without any increase in the overall size of the structure involved. Cell enlargement alone does constitute growth; this is particularly evident in plants in which there is a considerable net increase in cell size in maturing regions. Nonetheless, with few exceptions the continued growth of an organism requires the production of new cells and their enlargement, and these two processes are closely associated in space and time. Growth by itself will not lead to the formation of an organized body, but rather, at least in theory, to a homogeneous assemblage of cells. Clearly, the formation of an organized body implies that cells and groups of cells in different regions of the body have become structurally distinguishable and functionally distinctive. The changes that occur in these cells and groups of cells and bring about their distinctiveness constitute what is known as *differentiation*. Some biologists prefer to distinguish between those changes that lead to distinctive histological patterns – designated as cell differentiation, or histodifferentiation – and those that set apart major segments of the body or organs – designated as organogenesis. Because there is no reason to suppose that mechanisms underlying these two types of change are fundamentally different, it seems preferable to consider both as aspects of a general phenomenon of differentiation. There are cases in which growth can occur without differ-

entiation, and differentiation without growth, but it is almost always true that these two phenomena occur in intimate association. The development of an organized body depends upon the integrated activity of the two.

Although a book like this one ought to contain enough information and interpretation to be useful by itself, it is desirable that readers, particularly students, have access to the original studies in the field. For this reason, at the end of each chapter a selected bibliography is given, and reference is made to it in the context of the chapter. Although these lists are not comprehensive, they contain key reference works that offer the opportunity for a wider grasp of plant development. In addition, there are many extremely useful general reference works that are basic sources of information and points of view. A selected list of these references follows.

REFERENCES

- Balls, M., and F. S. Billett. 1973. *The Cell Cycle in Development and Differentiation*. Cambridge: Cambridge University Press.
- Barlow, P. W., and D. J. Carr. 1984. *Positional Controls in Plant Development*. Cambridge: Cambridge University Press.
- Bernier, G., J. Kinet, and R. M. Sachs. 1981. *The Physiology of Flowering*. Vol. 1 and 2. Boca Raton, Fla.: CRC Press.
- Bewley, J. D., and M. Black. 1985. *Seeds: Physiology of Development and Germination*. New York: Plenum.
- Burgess, J. 1985. *An Introduction to Plant Cell Development*. Cambridge: Cambridge University Press.
- Cutter, E. G. 1971. *Plant Anatomy: Experiment and Interpretation. Part 2: Organs*. London: Arnold.
- . 1978. *Plant Anatomy: Experiment and Interpretation. Part 1: Cells and Tissues*. 2d ed. London: Arnold.
- Dale, J. E., and F. L. Milthorpe. 1983. *The Growth and Functioning of Leaves*. Cambridge: Cambridge University Press.
- Esau, K. 1965. *Vascular Differentiation in Plants*. New York: Holt, Rinehart and Winston.
- . 1977. *Anatomy of Seed Plants*. 2d ed. New York: Wiley.
- Francis, D., and J. A. Bryant. 1985. *The Cell Division Cycle in Plants*. Cambridge: Cambridge University Press.
- Hallé, F., R. A. A. Oldeman, and P. B. Tomlinson. 1978. *Tropical Trees and Forests: An Architectural Analysis*. Berlin: Springer-Verlag.
- Johri, B. M. 1982. *Experimental Embryology of Vascular Plants*. New York: Springer-Verlag.
- . 1984. *Embryology of Angiosperms*. New York: Springer-Verlag.
- O'Brien, T. P., and M. E. McCully. 1981. *The Study of Plant Structure: Principles and Selected Methods*. Melbourne, Australia: Termarcarphi.
- Philipson, W. R., J. M. Ward, and B. G. Butterfield. 1971. *The Vascular Cambium: Its Development and Activity*. London: Chapman and Hall.

- Raghavan, V. 1986. *Embryogenesis in Angiosperms: A Developmental and Experimental Study*. Cambridge: Cambridge University Press.
- Roberts, L. W. 1976. *Cytodifferentiation in Plants: Xylogenesis as a Model System*. Cambridge: Cambridge University Press.
- Sinnott, E. W. 1960. *Plant Morphogenesis*. New York: McGraw-Hill.
- Tilney-Bassett, R. A. E. 1986. *Plant Chimeras*. London: Arnold.
- Torrey, J. G., and D. T. Clarkson. 1975. *The Development and Function of Roots*. New York: Academic Press.
- Vasil, I. K. 1984. *Cell Culture and Somatic Cell Genetics of Plants*. Orlando, Fla.: Academic Press.
- Wardlaw, C. W. 1968. *Morphogenesis in Plants: A Contemporary Study*. 2d ed. London: Methuen.
- Wareing, P. F., and I. D. J. Phillips. 1981. *Growth and Differentiation in Plants*. 3d ed. New York: Pergamon Press.
- Williams, R. F. 1975. *The Shoot Apex and Leaf Growth: A Study in Quantitative Biology*. Cambridge: Cambridge University Press.
- Yeoman, M. M. 1976. *Cell Division in Higher Plants*. New York: Academic Press.

CHAPTER

2

*Embryogenesis:
beginnings
of development*

We saw in the previous chapter that it is characteristic for morphogenetic events to continue throughout the life-span of most plants. This is in marked contrast to animal development, in which there is a concentration of morphogenetic phenomena in the embryonic stages. Nonetheless, like the animal, the vascular plant begins life as a single cell, the fertilized egg, and passes through an embryonic phase during which the fundamental body plan is laid down. Although it may be argued that all plants that develop from a single cell into a multicellular state pass through an embryonic phase, historically the term *embryo* has been restricted to those groups in which the early stages are enclosed within parental tissue and are presumed to be nutritionally dependent upon the parent organism. On this basis the bryophytes and the vascular plants often are designated the *Embryophyta*. In the bryophytes and the lower vascular plants there is no interruption of growth to mark the end of the embryonic phase, which is therefore rather ill defined. On the other hand, in the seed plants, embryonic development is considered to be terminated at the maturation of the seed, and this leads to a sharp distinction between the embryo and all postgermination stages.

Throughout the Embryophyta, as well as in some lower groups, plant development from a zygote alternates in the life cycle with development of a second plant body from a single-celled spore. Alternation of generations poses interesting morphogenetic problems because of the contrasting morphology of the two phases, each developed from a single cell but under different conditions. In discussing embryogenesis we shall be concerned primarily with the early or embryonic stages of development of the diploid zygote into a vascular sporophyte. The contrasting development of the haploid spore into the gametophyte will not be considered except as it sheds some light upon the factors that control the different development of the two generations.

PATTERNS OF EMBRYO DEVELOPMENT

In view of the fundamental similarity of somatic organization in the sporophytes of the principal groups of vascular plants, it is startling to

discover the diversity of embryonic patterns that lead to this organization (Wardlaw, 1955). The conclusion is unavoidable that these patterns in themselves have limited morphogenetic significance. Nevertheless, the various patterns must be recognized, because any functional generalizations must be compatible with them. The classification of embryo types based on the sequence of early cell divisions is a complex field with a voluminous literature and is one that has had an important bearing upon taxonomic and phylogenetic interpretations.

In this chapter we shall not examine examples of all these types; rather we shall describe several that reveal the range of embryonic diversity, with the hope of arriving at some general understanding of the principles of embryogenesis.

Embryo development in angiosperms

An excellent account of embryo development in a flowering plant has been given by Miller and Wetmore (1945) for *Phlox drummondii* (Figs. 2.1, 2.2). The first cell division is at right angles to the axis of the embryo sac and divides the zygote into a smaller *terminal cell* and a larger *basal cell*. The two cells each divide again in the same plane, giving rise to a four-celled filament. Divisions continue in each of these cells. The cell that lies nearest to the micropyle – the aperture through which the pollen tube grows prior to fertilization – divides in the same plane, producing a short, filamentous organ called the *suspensor*. The remaining three cells initiate the *embryo proper*. These cells undergo both longitudinal and transverse divisions and give rise to a globular mass in which the cells are arranged in regular tiers. At this stage the embryo, consisting of fewer than forty cells, is only four days old and is less than a quarter of a millimeter in length. By the fifth day the first evidence of histodifferentiation within the previously homogeneous globular embryo proper is detected. Divisions in the surface cells become progressively restricted to the anticlinal plane – that is, perpendicular to the surface – resulting in the appearance of a superficial layer called the *protoderm*. Shortly thereafter, internal differentiation becomes evident in a central column of densely staining, narrow, elongated *procambium* cells surrounded by a cylinder of vacuolated cells. Thus, at this early stage, the three principal tissue systems of the plant (*dermal, vascular, and fundamental*) have been initiated.

By the sixth day the first suggestion of the shoot apical meristem can be detected in the spherical embryo as an area of small, densely staining cells continuous with the central procambial core and at the pole of the embryo opposite the suspensor. A day or two later the two cotyledons appear as a result of localized concentrations of growth on either side of the shoot meristem but not in it, and the embryo passes into what

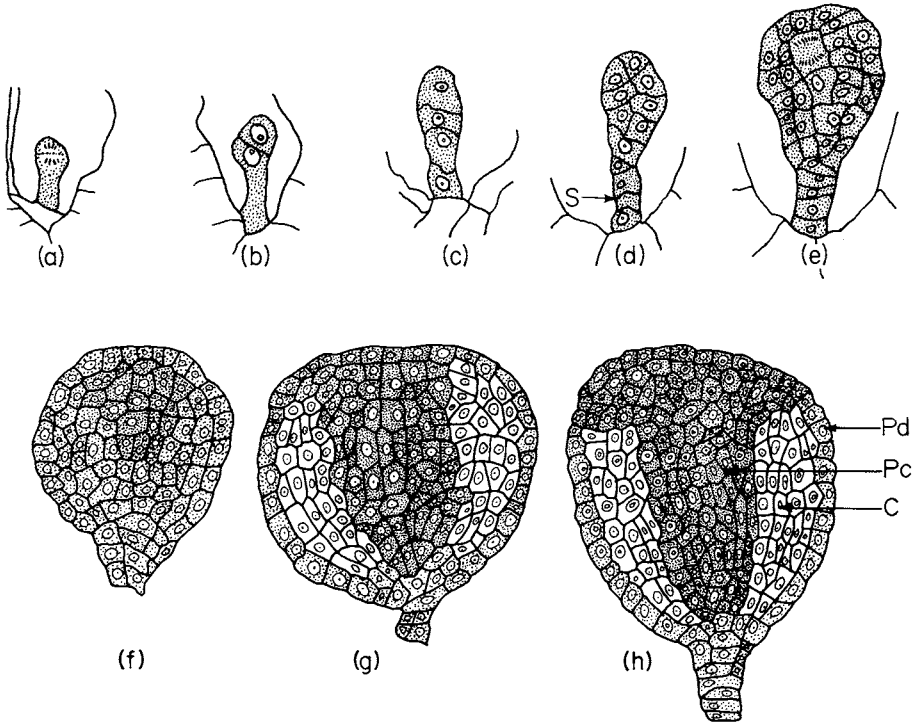


Figure 2.1. Embryo development in *Phlox drummondii*. (a) First division of the zygote. (b–e) Stages of the embryogeny in the first four days after fertilization. (f–h) Later stages showing differentiation of protoderm, procambium, and cortical parenchyma. The shoot apex is first distinguishable in (g). Key: C, cortical parenchyma; Pc, procambium; Pd, protoderm; S, suspensor. $\times 225$. (Miller and Wetmore, 1945.)

has been called the heart stage. Procambium continuous with that of the central core of the embryo axis extends into the cotyledons. As the cotyledons enlarge, the axis of the embryo also elongates, and at the end of the axis opposite the shoot apical meristem, periclinal divisions – that is, in a plane parallel to the surface – initiate a root cap beneath which the apical meristem of the primary root may be detected. The mature embryo is thus bipolar, with shoot and root apical meristems located at opposite extremities of its axis. The mature embryo, like the full-term animal embryo, possesses the fundamental organization of the adult body, but unlike the animal embryo, in which the major organs are present at least in rudimentary form, the shoot and root systems are represented only by their apical meristems.

On the basis of the planes of early cell divisions and the contributions

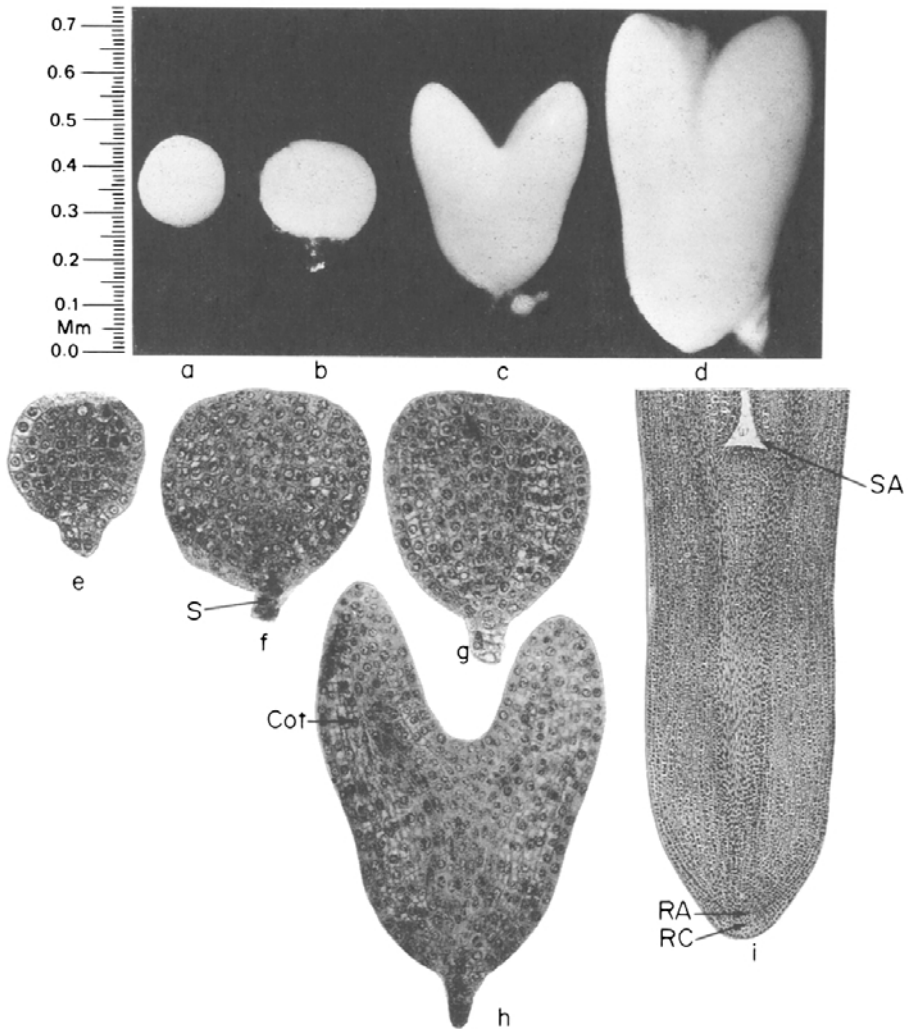


Figure 2.2. Embryo development in *Phlox drummondii*. (a–d) Dissected embryos showing globular, heart, and early torpedo stages. (e–h) Sections of embryos showing cellular detail of comparable stages. (e), (f), and (g) correspond to stages (f), (g), and (h) in Fig. 2.1. (i) Fully developed embryo showing shoot and root apices. Key: Cot, cotyledon; RA, root apex; RC, root cap; S, suspensor; SA, shoot apex; (a–d) $\times 60$, (e–g) $\times 160$, (h) $\times 95$, (i) $\times 25$. (Miller and Wetmore, 1945.)

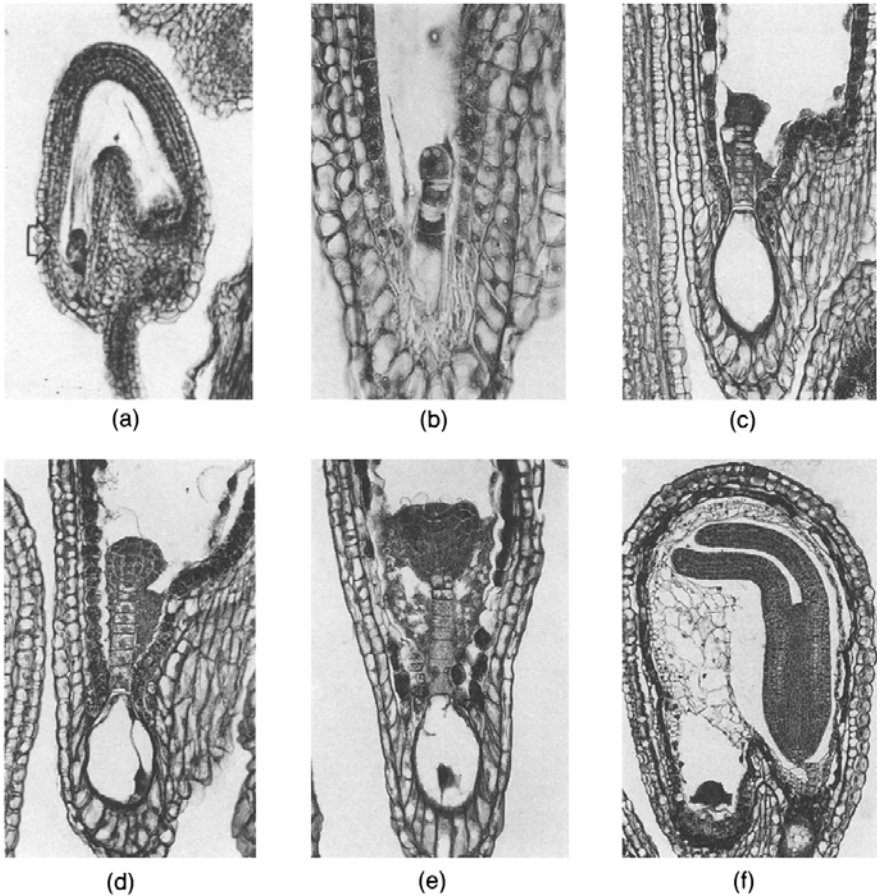


Figure 2.3. Embryo development in *Capsella bursa-pastoris*. (a) Zygote (arrow) enclosed in ovule. (b) Four-celled, filamentous embryo. (c) Early globular stage. (d) Late globular stage showing protoderm and fully developed suspensor. (e) Heart stage. (f) Maturing, bipolar embryo. (a) $\times 140$, (b) $\times 250$, (c–e) $\times 140$, (f) $\times 42$.

that their derivatives make to the development of the embryo, plant embryologists have recognized several patterns of embryonic development in the angiosperms (Maheshwari, 1950). The embryogeny of *Capsella bursa-pastoris* (shepherd's purse), which has been the subject of a number of detailed studies, shows a relatively precise sequence of early divisions and also contrasts with *Phlox* in features of later development (Fig. 2.3). Following the first transverse division of the zygote, the basal cell and its derivatives divide transversely to form a filamentous suspensor of six to ten cells. Meanwhile the terminal cell undergoes a lon-