

Chapter I

Problems of adaptation to a terrestrial environment

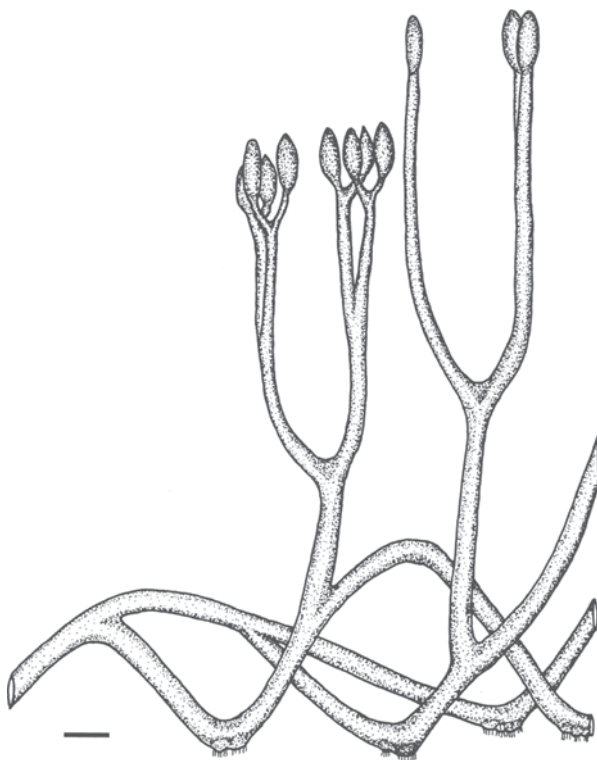
Perspective: the origin of vascular plants

Land plants, plants that complete their life cycle entirely in a terrestrial environment, are represented largely by bryophytes and vascular plants. In all taxa except seed plants, however, at least a thin film of water is required for fertilization; and even in two primitive groups of seed plants, the cycads and *Ginkgo*, fertilization is by free-swimming spermatozoids released into a liquid medium in the archegonial chamber. A few angiosperms, although terrestrial in origin, have reverted to an aquatic existence.

Vascular plants are by far the dominant groups on the Earth comprising over 255 000 species in contrast to about 22 000 species of bryophytes and approximately 20 000 species of algae. The first vascular plants appear in the fossil record in the late Silurian, about 420 million years ago, but their green algal ancestors are thought to have appeared nearly 400 million years earlier! Shared features comprise the major evidence that vascular plants, possibly also bryophytes, evolved from green algae: both synthesize chlorophylls a and b, both store true starch in plastids; both have motile cells with whiplash flagella, and both (but only a few green algae) are characterized by phragmoplast and cell plate formation following mitosis. A green alga, with these and other significant characteristics, that may provide a model of an algal ancestor of vascular plants is *Coleochaete*, a member of the Charophyceae. Features in addition to those listed above that lead to this conclusion are the development in *Coleochaete* of a zygote in which cell division begins while embedded in the gametophyte thallus, the presence of sporopollenin in the wall of the zygote, and the presence of lignin in the gametophyte. It is widely believed that the Embryophyta (bryophytes and vascular plants) and the Charophyceae evolved from a common aquatic ancestor. Detailed presentations of the evidence for this viewpoint and the nature of the presumed common ancestor can be found in major works by Graham (1993) and Niklas (1997, 2000).

The first, indisputable vascular plants were characterized by a conducting system containing xylem and phloem, a waxy cuticle,

Figure 1.1 Reconstruction of *Aglaophyton major*. Bar = 10 mm. From Edwards (1986). Used by permission of The Linnean Society of London.



epidermal stomata, and a reproductive system that produced **trilete spores** (spores with a triradiate scar resulting from their development in spherical tetrads) and probably containing sporopollenin in the walls. Such plants appear first in the late Silurian, but *Aglaophyton major* (see Edwards, 1986) from the Lower Devonian, which has morphologic and structural features of both some bryophytes and primitive vascular plants, provides perhaps the best available model of a vascular plant precursor. *Aglaophyton* was a small plant, probably no more than 180 mm (about 7 inches) high, composed of dichotomous, upright axes that branched from rhizomes on the surface of the substrate (Fig. 1.1). The epidermis of all axes was covered by a cuticle and contained stomata. Some upright axes were terminated in pairs of sporangia, containing small spores of one size only. Edwards suggested that the plant probably formed extensive mats, consisting largely of vegetative axes, but produced fertile axes, bearing sporangia, “at irregular intervals.” The rhizomes were probably vegetative axes that formed clusters of **rhizoids** (absorbing structures) where some axes arched over and contacted the substrate. One of the most interesting structural features of the axes of *Aglaophyton* was the central conducting strand. Although appearing superficially as a vascular strand consisting of xylem and phloem, and described that way by earlier workers, Edwards was unable to detect characteristic structural features of tracheary elements (that is, cells with secondary wall material deposited in the form of rings, helices, or a reticulum) or of sieve elements. Instead, he found three

regions of cells, an inner column of thin-walled cells surrounded by thick-walled cells, the walls of both of which were dark in color. These were enclosed by an outer zone of thin-walled cells with light-colored walls. He concluded that the two inner regions of cells with dark cell walls were probably analogous to tracheids but most similar to the **hydroids** (water-conducting cells) of some mosses and that the outermost cells with light-colored walls were analogous to sieve elements and very similar to the **leptoids** (photosynthate-conducting cells) of mosses. *Aglaophyton* was, therefore, a non-vascular plant sporophyte in which the sporophyte was the dominant phase in a system of pteridophytic (free-sporing) reproduction. In gross morphology and branching pattern, and the presence of an epidermis covered by a cuticle and containing stomata, it was very similar to primitive vascular plants that lived during Upper Silurian and Lower Devonian times. In its water- and photosynthate-conducting cells closely resembling, respectively, hydroids and leptoids, as well as in its small size and free-sporing reproduction, it closely resembled mosses. It is reasonable, therefore, to hypothesize that vascular plants evolved from this or plants of similar morphology and anatomy. (For detailed information on the earliest vascular plants, see Stewart and Rothwell (1993) and Taylor and Taylor (1993).)

Structural adaptations

During the past 350–400 million years many structural and physiological changes occurred as vascular plants evolved. Evolution on land posed many problems for plants such as *Aglaophyton* and its descendants not shared with their marine algal ancestors. In an aquatic environment, conditions are equable, and problems of water loss, support, absorption of water and minerals, and transport of water and minerals, photosynthate, and hormones, are either minimal or non-existent. This is true also, in large part, for very small plants such as most mosses. For example, the absence of efficient water-conducting cells in mosses apparently does not pose a problem for them since in many taxa water and minerals are absorbed through the external surfaces of the sporophytes and gametophytes. This is not unlike the situation in aquatic plants in which water and minerals are absorbed by all parts of the plant directly through the epidermis, which lacks a cuticle. Consequently, there is no need for a highly efficient system of transport of water and minerals. Likewise, with few exceptions, the transport of hormones and photosynthate is also not a problem since these substances are produced in all cells. On land, however, solar radiation, wind, and temperature extremes result in a much harsher environment. As *Aglaophyton* and its descendants evolved on land, structural features evolved as adaptations to both this harsher environment and to their increase in size.

Adaptations reducing water loss were the evolution of a three-dimensional, rod-like plant body which decreased the surface/volume

ratio, and an epidermis covered by a waxy cuticle largely impermeable to the passage of water. Although the evolution of a rod-like form was advantageous in restricting the surface area from which water could be lost, an optimal surface area in relation to volume was required through which transpiration as well as gaseous exchange could occur. The evolution of stomata in the epidermis allowed the exchange of O_2 and CO_2 , essential in respiration and photosynthesis, and by their ability to control the size of pores through which water vapor diffused, stomata also contributed to a restriction of water loss from the plant. Adequate surface area was also required, however, through which the plant could receive signals from the environment – signals such as light, temperature, or the presence of other organisms such as pathogens or symbionts as well as chemical signals from the atmosphere or from other organisms. We now know that chemicals produced by plants living today are also released through the surface and may elicit responses from other organisms such as moths and hummingbirds that function as pollinators. The response of plants to environmental signals, referred to as **signal transduction**, is a new and active area of research in plant biology.

Protection of spores and gametes, so very important in a terrestrial environment, was accomplished through the evolution of sporangia and gametangia enclosed in sterile jackets of cells. The spores themselves became encased in walls containing **sporopollenin**, a substance which restricts water loss and is highly resistant to decay.

Absorption of water and minerals from the soil was facilitated by the evolution of rhizoids and roots, the latter often containing symbiotic fungi forming mycorrhizae which, as we shall see in detail later, enhanced their absorptive function. Roots, in particular, also served to anchor the plant in its substrate and to prevent its displacement by wind and flowing water.

The effective transport of water and minerals as well as hormones, photosynthate, and other substances became increasingly important with increase in size of the descendants of *Aglaophyton* or other vascular plant precursors. This was accomplished by the evolution of complex vascular tissues containing tracheids and vessel members in the xylem and sieve cells and sieve tube members in the phloem, conducting cells especially adapted structurally for the transport of these materials. Associated with the evolution of cellular transport systems, specialized mechanisms evolved which facilitated the efficient transport of water and minerals from the roots to and out of the leaves of tall trees. Concurrently, mechanisms for the translocation of photosynthate and other assimilates throughout the plant evolved.

The problem of support of the plant body also became increasingly severe with increase in size and was solved by structural adaptations. In plants, or parts of plants, consisting largely of living tissues, support was provided by their enclosure by an epidermis as well as by turgor pressure within the cells. Ultimately, some of the functions of the epidermis were taken over by **periderm** (a major component of bark) consisting

largely of non-living cells, the walls of which are impregnated with **suberin** that restricted the passage of water through them. Support was also provided by the production of tissues consisting largely of non-living, longitudinally elongate cells with thick, lignified, cellulosic walls. The major supporting tissue in large plants is the xylem, consisting in pteridophytes and their ancestors as well as in gymnosperms primarily of tracheids, and in angiosperms of fibers and vessel members. **Lignin** in the cell walls increased the tensile strength of elongate cells comprising the xylem, thus endowing vascular plants with both strength and flexibility, so very important in conditions of high wind velocity.

The above-ground parts of the plant bodies of primitive vascular plants consisted primarily of radially symmetrical branching axes, all of which were photosynthetic. With the evolution of larger vascular plants consisting of stems and branches covered with bark, an adaptation that facilitated the process of photosynthesis was necessary. This was accomplished by the evolution of leaves which increased the surface/volume ratio of photosynthetic tissues in the plant. Structural adaptations in the leaves, such as the orientation of thin-walled elongate cells at right angles to the upper surface which channeled light at relatively high intensity into the leaves, and the complex system of intercellular channels which provided extensive wet surface area for the absorption of CO₂ facilitated efficient photosynthesis. For further information on adaptations by early plants to a terrestrial environment, and the evolution of plant body plans, please see Niklas (2000).

Preview of subsequent chapters

As we proceed through this book we shall encounter progressively detailed information on the structure and development as well as some aspects of evolution and function of the descendants of primitive plants such as *Aglaophyton*. We shall consider many members of the Embryophyta, including the Lycophyta (lycopods and their relatives), Sphenophyta (sphenophytes), and Pterophyta (ferns), but the major emphasis will be on the seed plants (gymnosperms and angiosperms). In order to provide an orientation to all who have had little or no training in plant anatomy, and to introduce some important concepts, the following chapter will be an overview of plant structure and development. If you have had a good course in introductory botany or biology, you may wish to proceed to later chapters. Chapters 3 and 4 present, respectively, basic information on the cell protoplast and the cell wall. The cell protoplast is usually covered in some detail in introductory courses, but the cell wall is often neglected. Consequently this book provides a fairly comprehensive discussion of its structure and development.

Chapter 5 presents very important information on apical meristems of the shoot, apical regions from which other cells and tissues in the

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shoot system are derived, and which provide to vascular plants their distinctive characteristic of indeterminate growth. Appendages such as leaves and lateral branches also are ultimately derived from the apical meristems. In Chapters 6, 7, and 8 we consider the structure and development of the various tissues and tissue systems that result from the activity of apical meristems. These chapters include, in sequence, discussions of the primary vascular tissues (xylem and phloem) that are embedded in the parenchyma of the pith and cortex; the architecture of the primary vascular system and its relationship to the arrangement of leaves; and the epidermis, the single layer of tissue that bounds all of these other primary tissues and tissue systems, and which forms an outer protective and supportive layer of the plant prior to the development of secondary tissues.

The second part of the book, Chapters 9 through 12, consists of discussions of the vascular cambium, a lateral meristem, the activity of which results in the formation of secondary vascular tissues, and the effects of their formation on the tissues and tissue systems produced by the apical meristems early in the development of the plant body. It also includes detailed presentations of the structure, development, and to a lesser extent evolution and function of the secondary xylem and the secondary phloem.

Chapters 13 through 18 deal with secretory structures and functions; anomalous stem and root structure; the outer protective tissues and tissue regions of stems that produce secondary tissues (the periderm and rhytidome) that comprise the bark; the structure, development, and function of leaves as well as a brief discussion of their evolution; a presentation of the structure, development, and function of roots, with some comments on their evolution; and finally, a chapter on reproduction which includes some basic life cycles, discussions of the structure and morphology of flowers, the structure and development of fruits and seeds, and some aspects of the ecology of reproduction in angiosperms.

The author hopes that you will enjoy this book and that by the end of your course in plant anatomy you will be as enthusiastic about this exciting field as he is.

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FURTHER READING

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Chapter 2

An overview of plant structure and development

Perspective: origin of multicellularity

Since early in the study of plants botanists have been interested in the structure, function, development, and evolution of cells, tissues, and organs. Because some green plants are very small and unicellular, but others are large and multicellular, the origin of multicellularity in plants also has been of great interest to botanists. Among the green algae from which higher plants are thought to have evolved, some colonial taxa such as *Pandorina*, *Volvox*, and relatives consist of aggregations of motile cells that individually appear identical to apparently related unicellular forms (Fig. 2.1). Consequently, it was concluded early in the history of botany, and widely accepted, that multicellular plants evolved by the aggregation of unicellular organisms. This viewpoint led to the establishment of the **cell theory of multicellularity** in plants which proposes that cells are the building blocks of multicellular plants (Fig. 2.2). As early as 1867, however, Hoffmeister proposed that cells are simply subdivisions within an organism. This viewpoint, supported and expanded upon in 1906 by Lester Sharp at Cornell University, has been elucidated and clarified more recently by Hagemann (1982), Kaplan (1992), and Wojtaszek (2000) among others. These workers conclude on the basis of abundant evidence that a unicellular alga and a large vascular plant are organisms that differ primarily in size and in the degree to which they have been *subdivided* by cells (Fig. 2.2). This **organismal theory of multicellularity** has gained many adherents within the past several decades (see Kaplan, 1992), and is of great importance because of ways in which it has influenced the thinking of botanists about the processes of development.

A primary and convincing basis for the organismal theory is the nature and result of cell division in plants. Following mitosis and cell plate formation, the protoplasts of the two resulting daughter cells maintain continuity through highly specialized cytoplasmic strands called **plasmodesmata** (Fig. 2.3) (see Chapter 4 for a detailed discussion of plasmodesmata). Thus, although the plant is blocked off in regions called cells, the plasmodesmata provide for an interconnected system

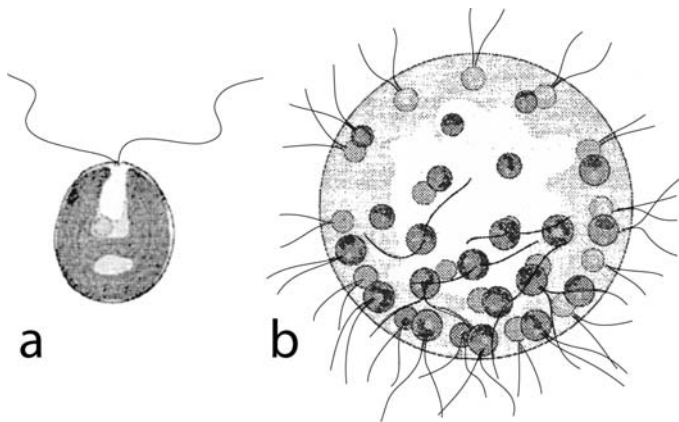


Figure 2.1 Unicellular and colonial body plans among green algae. (a) *Chlamydomonas* sp. (b) *Pandorina morum*. From Niklas (2000). Used by permission of Oxford University Press.

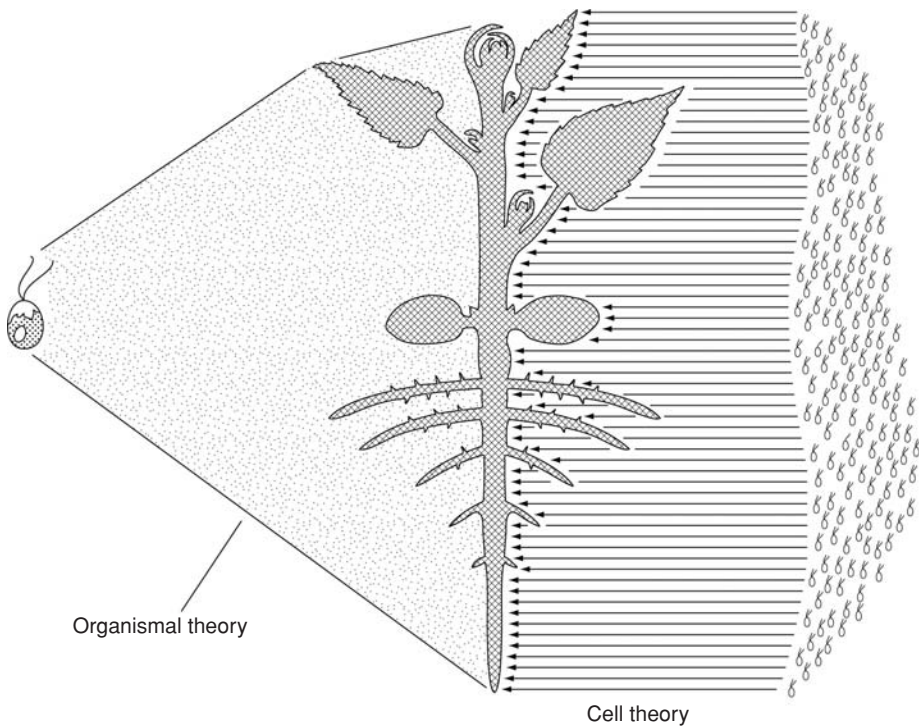
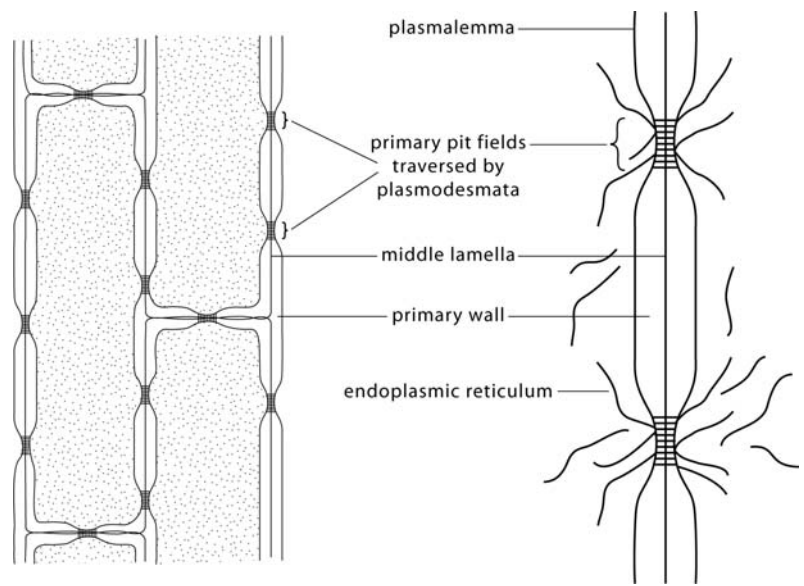


Figure 2.2 Diagram showing the relationship between a unicellular and a multicellular organism according to the organismal theory of multicellularity and the cell theory. From Kaplan (1992). Used by permission of the University of Chicago Press. © 1992 The University of Chicago. All rights reserved.

of protoplasts called the **symplast**. The plasmodesmata function as passageways for communication between living cells, that is, for the transmission between cells of molecules of varying size including even large molecules such as proteins and nucleic acids (e.g., Lucas *et al.*, 1993; Kragler *et al.*, 1998; Ehlers and Kollmann, 2001). It has become

Figure 2.3 Diagrams of primary pit fields traversed by plasmodesmata in primary cell walls. The plasmodesmata connect the protoplasts of adjacent parenchyma cells.



clear in recent years that this communication between cells has a profound influence in plant development (e.g., Verbeke, 1992). These and other workers believe that plasmodesmata may exert a “controlling influence” on cell differentiation, tissue formation, organogenesis, and specialized physiological functions.

For more detailed discussions of evidence in support of the organismal theory of multicellularity in plants and the significance of this theory in understanding plant development, see Kaplan and Hagemann (1991), Niklas and Kaplan (1991), Kaplan (1992), and Wojtaszek (2000).

Let us now look at the vascular plant body in general terms and obtain an overview of its structure and development. In subsequent chapters we shall consider in more detail many aspects of plant structure and development as well as of function and evolution.

Some aspects of the shoot system of the vascular plant

The vascular plant consists of an aerial shoot system and, typically, a subterranean root system (Fig. 2.4). The **shoot system** consists of a main axis that bears lateral branches. Leaves may be borne on both the main axis and lateral branches in plants that complete their life cycle in one growing season, but in those that live for several to many years, leaves are usually found only on the parts of lateral branches that have developed in the past year or the last several years. For example, in deciduous plants (e.g., many woody angiosperms), leaves develop only on the most distal segments of the laterals, i.e., the parts produced during the most recent growing season (Fig. 2.5) and will fall from the plant at the end of the same growing season. In most conifers and other