CHAPTER 1

Morphology and tissue systems: the integrated plant body

General background

Because each organ of the plant will be discussed in detail in later chapters, this section is intended only to be a reminder of basic plant structure and arrangements of tissue systems. It is not intended to be comprehensive, and by its very nature it oversimplifies the complex and wide range of form and organization existing in the higher plants. When a specialized term is first used, it is normally defined. The glossary forms an essential part of the book, and should be consulted if the meaning of a term is not clear.

This book concentrates on the vegetative anatomy of land plants, and in particular on monocotyledons and dicotyledons (flowering plants, angiosperms, with the seeds enclosed in carpels). Some anatomical features of conifers (gymnosperms – plants with seeds but without carpels fruits, enclosing the seed) are also described. Monocotyledons (Fig. 1.1) are flowering plants that when the seed germinates start life with one seed leaf, and lack the tissues that form new (secondary) growth in thickness, the vascular cambium, and a long-lived primary root. Examples include the grasses, orchids, palms and lilies. Dicotyledons (Fig. 1.2) are also flowering plants but have two seed leaves, and like the conifers have stems that generally have the ability to grow in thickness through a formal vascular cambium, and have a long-lived primary root. Examples of dicotyledons include the bean, rose and potato families, and the conifers include such plants as pines, larches and araucarias. There are, of course, other features that distinguish the angiosperms from gymnosperms (e.g. reproductive structures and reproductive cycle).

The plant organs are shown in Figs 1.1 and 1.2. Most land plants have roots, which anchor them in the ground, or attach them to other plants (as in epiphytes). Roots also absorb water and minerals. Roots first arise in the
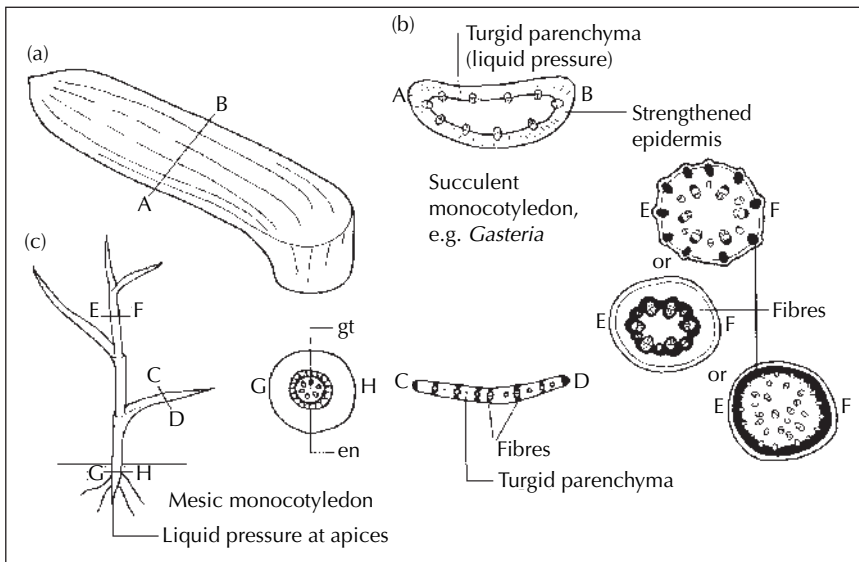
Fig. 1.1 Some mechanical systems in monocotyledons. (a) A fleshy leaf of *Gasteria*; note lack of sclerenchyma in the section (b). (c) A mesic monocotyledon, C–D shows one type of sclerenchyma arrangement in leaf TS; E–F shows three of the main types of sclerenchyma arrangements in the stem TS; G–H shows a typical root section in which most strength is concentrated in the centre. en, endodermis; gt, ground tissue, which may be lignified.
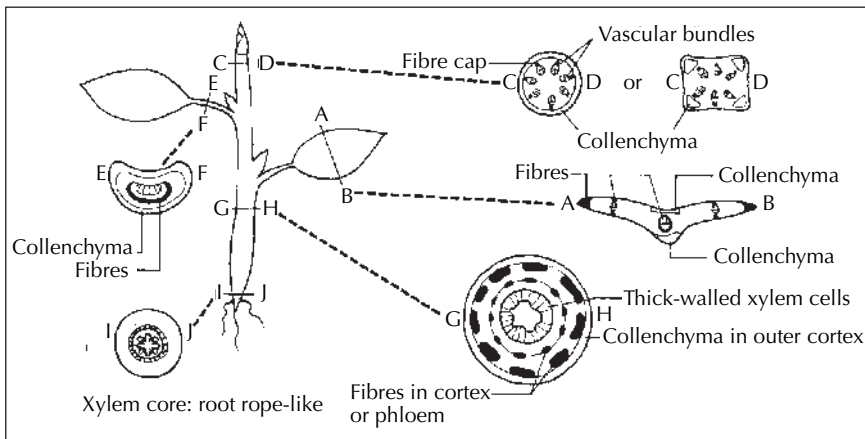
Fig. 1.2 Some mechanical systems in dicotyledons. A schematic plant with position of sections indicated. Liquid pressure occurs in turgid cells through the plant. Collenchyma is often conspicuous in actively extending regions and petioles. Sclerechyma fibres are most abundant in parts that have ceased main extension growth. Xylem elements with thick walls have some mechanical function in young plants and give a great deal of support in most secondarily thickened plants.

embryo and are there attached to the stem through a specialized region called the hypocotyl. Later in development if growth in thickness occurs, the hypocotyl becomes obscured. Many species grow additional roots, called adventitious roots, because they arise from other parts of the plant (although some roots themselves can also give rise to adventitious roots, but these do not develop from the normal sites for secondary roots). When leaves are present, they arise from the stem, either from the apical meristem (see next chapter), or from axillary bud meristems. Their particular arrangement (phyllotaxy) is usually recognizable, for example opposite one another, alternate or in an obvious spiral. Buds may be present in the axils of leaves, that is, between the leaf and the stem, close to where they join. Sometimes buds develop from other parts of the plant; these are called adventitious buds.

Adaptation to aerial growth

To understand the structure – morphology and anatomy – of land plants we have to remember that plant life started from single-celled organisms in an aquatic environment. There are still many thousands of different species of unicellular algae both in water and exposed – on tree trunks, leaves, soil and rock faces for example, in suitably moist places. Evolution of algae in the water has produced some very large, multicellular forms, for example *Laminaria* species, kelps. These large plants are fine in water, but lack the adaptations necessary for terrestrial life. They need to be bathed in water, which is a source of dissolved nutrients. Because they can absorb nutrients over most of their surface area, there is no need for a complex internal plumbing system, like the xylem (woody tissue) and phloem (cells adapted to conduct synthesized materials in the plant) in vascular bundles of land plants. They lack roots, but have holdfasts, structures adapted to anchor them to a firm substrate, but which are not absorbing organs for minerals and water, such as roots usually are. They lack a waterproof covering, a modified outer layer of epidermal cells of land plants, and rapidly desiccate if exposed to the air. Their mechanical support comes from the surrounding water, so they do not need the woody tissue (xylem) or fibres (elongate, thick-walled cells with tapered ends whose cell walls become strengthened with lignin, a hard material, at maturity; form part of the sclerenchyma) of land plants. True, they are tough and very flexible, and most can survive violent wave action. Even their reproduction depends on the release of male and female gametes into the water around them.

Some types of land plants still rely on a film of water for their male gametes to swim in to reach the female gamete and effect fertilization, for

example mosses and ferns, but the higher plants like gymnosperms and angiosperms have their male gametes delivered in a protective package, the pollen grain, to a receptive female part of the cone or flower.

There is a very wide range of land habitats, and land plants show a remarkable range of shapes and sizes. This book is mostly about the anatomy of flowering plants (angiosperms), and the vast majority of these share distinct vegetative organs that are readily recognized. They are leaf, root and stem (Figs 1.1, 1.2). These organs cope with the need to obtain, transport and retain enough water to help prevent wilting, carry dissolves minerals and keep the plants cool when necessary. Most land plants contain specialized cells and tissues for mechanical support and others for movement within the plant of materials they synthesize. The tough skin (epidermis, together with a cuticle and sometimes waxy materials) prevents water loss but permits gas exchange. Small pores in the epidermis of most leaves and young stems can be opened and closed and regulated in size (see Chapter 6 for details). These are called stomata and they regulate the rate of movement of water and dissolved minerals through and out of the plant. Sometimes the epidermis is the main part of the mechanical system as well, and holds the main leaf or stem material inside under hydraulic pressure.

In many plants, the strength of the 'skin' is supplemented by tough mechanical cells arranged in mechanically appropriate areas. These are forms of sclerenchyma cells with lignified walls: fibres which are elongated cells and sclereids, which are usually relatively short; a range of types exists (see the Glossary). Collenchyma is also a supporting or mechanical tissue which occurs in young organs and in certain leaves; the walls are mainly cellulosic. Here walls are thickest in the angles between the cell walls, or in lamellar collenchyma wall thickening is found mainly on anticlinal cell walls; see below for details.

Plants submerged in water are afforded some protection from damaging ultraviolet (UV) light. Land plants need other mechanisms to prevent UV damage. The green pigment, chlorophyll, is readily damaged by UV. Since this pigment and its cohort of specialized enzymes is responsible for transforming the energy of sunlight through its action on CO_2 and H_2O into sugars, the starting point for nearly all stored organic energy on earth, it is vitally important that the UV screening methods developed are effective.

All green plants need light for photosynthesis. Plants have evolved different strategies which bring leaves into a good position for obtaining the sunlight. Some (annuals, ephemerals) put out their leaves before others neighbouring plants, complete their annual or shorter cycle and form seed for the next generation. Others retire to a dormant form (some perennials and biennials) at a time when they may be shaded by taller vegetation. Many

species develop long stems or trunks and expose their leaves above the competition (some are annuals or biennials and but most are perennials). Some species do not have mechanically strong stems, but use the support provided by those which do, climbing or scrambling over them (they can be either annuals or perennials). Biennials are plants with a two-year life cycle. They build up a plant body and food reserves in the first year, and then flower and fruit in the second.

In summary, the main factors which all terrestrial plants with aerial (above-ground) stems and their associated leaves have to overcome are:

1 Mechanical, i.e. support must be provided in one way or another so that a suitable surface area with cells containing chloroplasts can be exposed to the sunlight to intercept and fix solar energy. These chlorenchyma cells may be on the surface, or just beneath translucent layers of cells. See below for more detail of the cell types that give mechanical strength. Secondary growth in thickness is another strategy that provides mechanical strength to parts both above and below ground. The growth in thickness may be relatively small in annuals, but in perennial plants it may be extensive, and requiring the use of large quantities of energy in its production. When present, the way secondary growth occurs differs between monocots and dicots.

2 Risk of excess water loss, i.e. they must be provided with protection against too much water loss from the exposed surfaces. This is generally done by a combination of a waxy outer layer and a fatty cuticle above an epidermis (the outer skin). Because water has to evaporate from some exposed surfaces so that movement of water and dissolved minerals can take place through the plant (transpiration), most leaves, and stems which retain the epidermis, have regulated pores, stomata, which can be opened and closed in response to prevailing conditions.

3 The ability to move water and minerals from the soil (transpiration) through the roots to regions where they can be combined with other materials to build the plant body, and the movement of synthesized food material from the site of synthesis to places of growth or storage and from the stores to growing cells (translocation). Of particular interest is the level of structural and physiological control of the phloem loading process. Epiphytes are attached by their roots to other plants, and obtain their water and minerals in different ways.

4 Reproduction, placement of reproductive organs enabling the pollen or gamete receptor mechanism to operate successfully, and after fertilization and spore/seed production, ensuring dispersal of the propagules.

The first three issues outlined above are dealt with by well-organized (if complex) systems in the higher plants, and will be summarized here. The fourth, reproduction, is outside the scope of this book. Secondary growth is discussed in Chapter 2, under lateral meristems.

Mechanical support systems

1 Using inflated or turgid, thin-walled cells (parenchyma): these are present in growing points, and the cortex and parenchymatous pith of many plants. They constitute the bulk of many succulent plants, for example, *Aloe*, *Gasteria* leaves, *Salicornia* from salt marshes and *Lithops* from desert regions. The cell wall acts as a slightly elastic container; internal liquid pressure inflates the cell so that it becomes supporting, like the air in an inflated car tyre. Its support properties depend on water pressure, so a water shortage can lead to a loss of support and wilting. Some fairly large organs can be supported by this system, but they usually rely on the additional help of devices that reduce water loss, such as a thick cuticle, and perhaps also thick outer walls to the epidermal cells, and specially modified stomata. A strong epidermis is particularly important, because it acts as the outermost boundary between the plant cells and the air. A split in the skin of a tomato, for example, rapidly leads to deformation of the fruit, or a cut in the succulent leaf of a *Crassula* or *Senecio* rapidly opens up. Not many plants rely on the turgid cell and strong epidermis principle alone.

2 Both monocotyledons and dicotyledons and have specially developed, elongated, thick-walled fibres, in suitable places, which assist in mechanical support. Alternatively, they have especially thick-walled, generally elongated parenchyma cells (also sometimes called prosenchyma); or, in those primary parts of the stem where growth in length is continuing, collenchyma cells may be present. Although there are only a few common ways in which specialized mechanical supporting cells are arranged in the stem, leaf or root, it is the variations on these themes which are of particular interest to those who have to identify small fragments of plants, or make comparative, taxonomic studies. The variations will be dealt with in detail in the chapters dealing with each organ. Obviously, to be effective the mechanical system must be economical in materials, and the cells must not be arranged in such a way as to hinder or impede the essential physiological functions of the organs.

The mechanical systems develop with the early growth of the seedling. Whilst turgid cells are the only means of support at first, collenchyma may rapidly become established, particularly in dicotyledonous plants. This tissue is concentrated in the outer part of the cortex, and is frequently associated with the midrib of the leaf blade, and the petiole.

Collenchyma is essentially the strengthening tissue of primary organs, or those undergoing their phase of growth in length. The cells making up this tissue have thickened cellulosic walls at their angles, are rich in pectin and are often found with chloroplasts in their living protoplasts.

Sometimes the only other mechanical support is provided by the wood (xylem) composed of tracheids (imperforate tracheary elements, i.e. cells with intact pit membrane q.v., between them and adjacent elements of the vascular system), as in most gymnosperms, or by the tracheids, vessels (tube-like series of vessel elements or members with perforate common end walls; vessel elements are the individual cell components of a vessel, with perforated end walls) and xylem fibres of the angiosperms. However, far more commonly there are also fibres outside the xylem (extraxylary fibres) which are arranged in strands or as a complete cylinder, such as in *Pelargonium* which can give considerable strength to herbaceous plants, and particularly in herbaceous monocotyledons in their stems and leaves. The much elongated fibres, with their cellulose and lignin walls, are not so flexible and do not stretch as readily as does collenchyma; consequently they are often found most fully developed in those parts of organs that have ceased growth in length.

Figure 1.1 shows some fibre arrangements in monocotyledon stems and leaves. In the leaf, fibres commonly strengthen the margins (e.g. *Agave*) and are found as girders or caps associated with the vascular bundles. In the stem, strands next to the epidermis can act rather like the iron or steel reinforcing rods in reinforced concrete. Together with a ribbed outline that they often confer on the stem section, they produce a rigid yet flexible system with economy of use of strengthening material.

Tubes are known to resist bending more effectively than solid rods of similar diameter; they also use much less material than the solid rod. It is not surprising then, that tubes or cylinders of fibres commonly occur in plant stems. They may be next to the surface, further into the cortex, or may occur as a few layers of cells uniting an outer ring of vascular bundles (Fig. 1.1).

The various arrangements within leaves, stems and roots will be discussed in more detail in Chapters 4–6. Mention must be made here that in some monocotyledon stems individual vascular bundles scattered throughout the stem can each be enclosed in a strong cylinder of fibres, which form a bundle sheath. Each bundle plus its sheath then acts as a reinforcing rod set in a matrix of parenchymatous cells and with a sieve cell centre so the whole unit acts as a hollow cylinder with maximum efficiency of both transport and strength.

Fibres or sclereids in dicotyledon leaves are also often related to the arrangement of the veins in the lamina and to the petiole vascular traces. These are shown in Fig. 1.2. The concentration of strength in an approximately centrally placed cylinder or strand in the petiole permits considerable torsion or twisting to take place as the leaf blade is moved by the wind, without damage occurring to the delicate conducting tissues. Primary dicotyledonous stems may have fibres in the cortex and phloem. The subterranean roots of both monocotyledons and dicotyledons have to resist

different forces and stresses from those imposed on the aerial stems – tensions or pulling forces, as opposed to bending forces. The concentration of strengthening cells near the root centre gives it rope-like properties. See Chapter 4 for a further development of these themes.

The transport systems

It is not possible to present a simple, comprehensive model to demonstrate the wide range of arrangements of vascular systems that occur in vascular plants, or in either dicotyledons or monocotyledons for that matter. Dicotyledons that are composed of wholly primary tissues tend to be a little more stereotyped than monocotyledons, but even then there is a very wide range of arrangements.

The essential elements of both systems are the xylem, concerned with transport of water and dissolved salts, and the phloem, which translocates synthesized but soluble materials around the plant to places of active growth or regions of use or storage. Xylem strands and phloem strands are normally associated and together form the vascular bundles, and are often enclosed in a sheath of fibres, and in addition, in some instances, an outer sheath of parenchyma cells (the bundle sheaths). Vascular bundles make up the 'plumbing system' of primary tissues, and organs without secondary growth in thickness.

In the apex (tip) of the shoot and root, where vascular tissue is not yet developed, soluble materials and water move from cell to cell through specialized very fine strands of protoplasm (called plasmodesmata) in these relatively unspecialized zones. Not far back from these growing points, however, more formal conducting systems are needed to cope with the flow of assimilate and water. Procambial strands, strands of elongated, thin-walled cells which are the precursors of the vascular bundles, are seen first and then, further from the tips, differentiation of protophloem (first formed primary phloem) alone followed by protoxylem (first formed primary xylem) and then by the metaphloem and metaxylem (next formed phloem and xylem cells respectively). The protoxylem and metaxylem, protophloem and metaphloem together constitute the primary vascular tissues. In most dicotyledons, the newly formed strands join the previously formed vascular bundles in the stem through a leaf or branch gap, which is composed of parenchyma cells, and 'breaches' the harder tissues associated with the plumbing of the stem.

In most dicotyledons the leaf lamina (blade) has a midrib to which are connected the lateral veins. The latter form a network composed of major and minor systems. The midrib is directly connected to the petiole trace, the vascular system of the petiole or leaf stalk. This enters the stem and joins into the main stem system through a leaf trace gap as described above. In the primary stem, all vascular bundles are separate from one another

except at the nodes – those parts of the stem where one or more leaves are attached. Vascular bundles in the stem may remain separate in many climbers, e.g. *Cucurbita*, *Ecballium*, but in most dicotyledons the bundles become joined into a cylinder by growth of secondary xylem and phloem from vascular cambium (a lateral meristem composed of thin-walled cells from which the secondary vascular tissues develop); it is made up of the fascicular cambium forming within the vascular bundle and the interfascicular cambium between vascular bundles.

A complex rearrangement of tissues takes place in the primary plant where the systems of the stem and root meet (hypocotyl). In the stem vascular bundles, the phloem is normally to the outer side of the xylem in the majority of plants. In the root, as seen in cross-section, the xylem is central, and may have several lobes or poles, with the phloem situated between these. After secondary growth has taken place, the hypocotyl becomes surrounded by secondary xylem and phloem, and the shoot and root anatomy become more similar. Secondary growth is discussed in Chapter 3.

Transfer cells are specialized parenchymatous cells found in various parts of the plant, but in particular, in regions where there is a physiological demand for transport, but where more normal phloem or xylem cells are not in evidence. A good example is the junction between cotyledons (first seedling leaves) and the shoot axis in seedlings. Transfer cells may also be present near the extremities of veins, or near to adventitious buds (buds developing in an unusual position, e.g. on a stem in addition to or replacing those in leaf axils, or buds on root or leaf cuttings).

Thin sections of the walls of transfer cells show them to have numerous small projections directed towards the cell lumen (the part of the cell to the inner side of and enclosed by the cell walls). These greatly increase the plasmalemma–cell wall surface interface. a site of metabolic activity concerned with the rapid, energy-mediated movement of materials between adjacent cells. The projections are so fine that conventional sections with a rotary microtome are too thick for them to be seen.

Monocotyledons are quite different from dicotyledons in their vasculature. Leaf and stem are commonly much less readily separable as distinct organs. There is no secondary growth by a true vascular cambium, so a cylinder of vascular tissue does not form. When secondary growth occurs, as in *Dracaena* and *Cordyline*, it is by means of specialized tissue, situated near to the stem surface, which forms complete, individual vascular strands and additional ground tissue.

Vascular bundles are usually arranged in the stem with the xylem pole facing towards the stem centre (but this is not invariably so). The arrangement of leaf vascular bundles is very variable. Grasses and some *Juncus* species, for example, often have one row as in Fig. 1.3. Some of the other types of arrangement are discussed in Chapter 6.
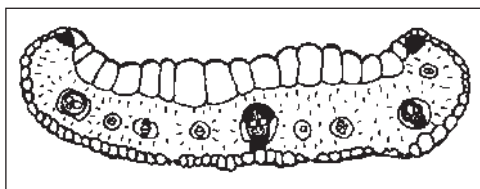
Fig. 1.3 *Juncus bufonius* leaf (TS, ×48), showing one row of vascular bundles, with the xylem poles directed towards the adaxial surface. Note the marginal sclerenchyma strands and the difference in size between adaxial and abaxial epidermal cells. Each small vascular bundle has a parenchyma sheath; in larger bundles sclerenchyma caps interrupt the parenchyma sheath.

Because there is no vascular cylinder in monocotyledons, where leaf traces (bundles) enter the stem they do not form gaps. They may join at nodes, where all the bundles at that particular level of the stem form a type of plexus, as in aloes. Sometimes, in stems with nodes, the leaf traces may continue downwards from their points of entry into the stem for a complete internode before joining the nodal plexus below (e.g. *Restio*, *Leptocarpus*, Restionaceae). In other plants without nodes (e.g. palms), the leaf traces follow a simple path curving inwards towards the stem centre, and then gradually 'move' towards the outer region of the stem lower down. These leaf traces join onto the main bundles by small, inconspicuous bridging bundles. This system is beautiful in its simplicity, but very difficult to analyse because there are so many (several hundred) vascular bundles even in the narrow portion of a stem of a small palm like *Rhapis*. As one follows the course of bundles in a palm, they are seen to spiral down the stem.

The primary root does not develop in a majority of monocotyledons. Its function is usually taken over by numerous adventitious roots that arise at an early stage, usually at the nodes, and join the stem vascular system in what frequently appears as a jumble of vascular tissue with very short elements both in the phloem and xylem.