

Plant Anatomy

Gregor Barclay, *University of the West Indies, St Augustine, Trinidad and Tobago*

Plant anatomy describes the structure and organization of the cells, tissues and organs of plants in relation to their development and function.

Introduction

Higher plants differ enormously in their size and appearance, yet all are constructed of tissues classed as dermal (delineating boundaries created at tissue surfaces), ground (storage, support) or vascular (transport). These are organized to form three vegetative organs: roots, which function mainly to provide anchorage, water, and nutrients; stems, which provide support; and leaves, which produce food for growth. Organs are variously modified to perform functions different from those intended, and indeed the flowers of angiosperms are merely collections of leaves highly modified for reproduction. The growth and development of tissues and organs are controlled in part by groups of cells called meristems. This introduction to plant anatomy begins with a description of meristems, then describes the structure and function of the tissues and organs, modifications of the organs, and finally describes the structure of fruits and seeds and how these are modified for dispersal. **Figure 1** presents an illustration of the structures of a typical plant.

Meristems

Because they are rooted to one spot, plants must adapt to changing conditions in order to survive. They must be able to rejuvenate parts that are damaged or lost as they grow, and continue the cycle of producing flowers and setting seed. For these reasons plants are able to renew themselves continually through localized growth, a process that occurs in meristems. These are sources of undifferentiated, genetically sound, cells.

Determinate meristems are designed to produce structures of a certain size, such as leaves and flowers. The great similarity of the leaves on a tree results from the effectiveness of determinate meristematic activity in creating copies of structures. Indeterminate meristems are never-ending sources of new cells, allowing increase in length (apices) or girth (cambium).

Meristematic activity arises early in embryogenesis. In some plants, when the ovule reaches the 16-cell stage of development, there is already an outer layer consisting of eight of these cells. This layer is the first discernible protoderm, which is the primary meristem giving rise to the epidermis of the plant. Two other fundamental primary

Introductory article

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meristems arise in the embryo, the ground meristem, which produces cortex and pith, and the procambium, which produces primary vascular tissues. In shoot and root tips, apical meristems add length to the plant, and axillary buds give rise to branches. Intercalary meristems, common in grasses, are found at the nodes of stems (where leaves arise) and in the basal regions of leaves, and cause these organs to elongate. All of these are primary meristems, which establish the pattern of primary growth in plants.

Stems and roots add girth through the activity of vascular cambium and cork cambium, lateral meristems that arise in secondary growth, a process common in dicotyledonous plants (**Figure 2**). Many monocotyledonous plants have primary meristems alone, and lack true secondary growth. Cambium is in essence an intercalary meristem because it lies between its derivatives. Vascular cambium normally creates xylem to the inside and phloem to the outside of stems and roots (just as cork cambium lies between its derivatives). But in time, primary intercalary meristems stop producing new cells and disappear, whereas cambium is essentially indeterminate in its activity. The activity of the vascular cambium is complex. It produces more xylem than phloem, and thus it expands in circumference and it must add new cells by radial divisions to maintain the integrity of the cambial cylinder.

Plants are prone to mutation because they are potentially long-lived and also because they are subjected to ionizing ultraviolet light from the sun. Mutations are most likely to occur during cell division, so the fewer cell divisions plants need for growth, the better. Meristems let the plant avoid repetitive cell divisions, reducing the possibility for mutation. But because plants have growth localized in meristematic areas, these are at risk of accelerating mitotic mutations if all they do is create cell lines (cells of the same type) by endless cell division. Plants avoid cell lines by having multistep meristems. This multistep meristem produces secondary vascular tissue (see **Figure 3**).

This delegation of roles makes cell lines much shorter. Endlessly repeating cell divisions are not eliminated, but they tend to occur as the end product of the meristem, that is, identical cells that do not divide further. For example,

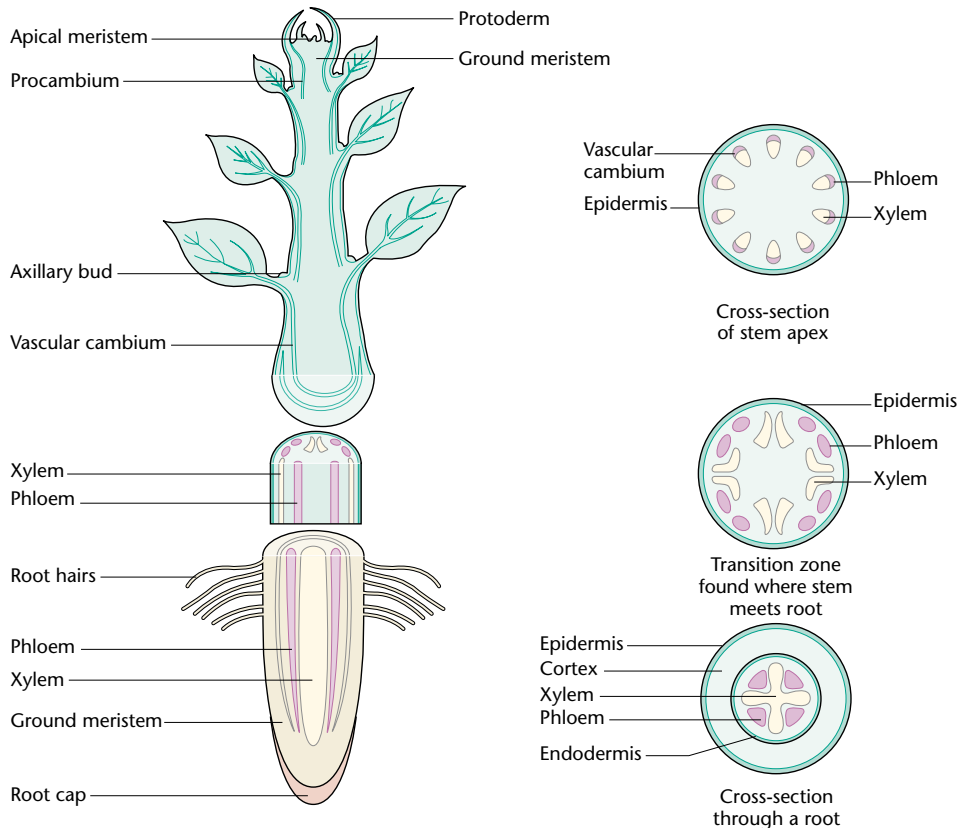


Figure 1 Longitudinal section through a typical plant and cross-section of the specific areas.

cork cells are produced in great numbers by the cork cambium and they are dead when functional. It does not matter if some of these cells are mutated because their genes are not passed on.

Reduction in mutation enhances the potential for plants to grow indefinitely. While ‘Eternal God’ a coast redwood (*Sequoia sempervirens*) in California has lived for more than twelve millennia, it is still young when compared to clonally reproducing specimens of King’s holly (*Lomatia tasmanica*) in the wilderness of Tasmania that are 43 400 years old. Meristematic activity in these and other plants of great age has allowed them to achieve states of near immortality.

Dermal Layers

All plants are wrapped in protective layers of cells, and other cell layers occur inside them. An epidermis, which may be defined as the outermost cell layer of the primary plant body, entirely covers herbaceous plants: leaves, stems, and roots all have an epidermis. Although usually just one cell thick (uniseriate), some plants have a multiple

(multiseriate) epidermis many layers thick. Epidermal cells may live for many years, and are modified in diverse ways.

The epidermis forms an interface between the plant and its environment. It is coated with cutin, a complex fatty substance that forms the cuticle and is indigestible by pathogens. The cuticle is impregnated with long chained waxes, which render it very impermeable to water. The cuticle is clear, like the epidermal cells it covers, allowing light to reach photosynthetic tissues beneath. Also, the cuticle selectively protects the plant from mutagenic, ultraviolet sunlight.

The epidermis has stomata that allow gas exchange between the plant and the air surrounding it. Each stoma consists of a pair of bean-shaped guard cells that can bend apart to create a stomatal pore. Guard cells have large nuclei and numerous chloroplasts (usually they are the only epidermal cells to have chloroplasts). In most monocotyledonous plants, the guard cells are dumbbell shaped.

Trichomes arise from epidermal cells that extend outward, typically dividing repeatedly to form a single file of cells. Trichome functions include shading the plant surface from excessive light, reducing air movement (and thus excessive desiccation), and protecting the plant from

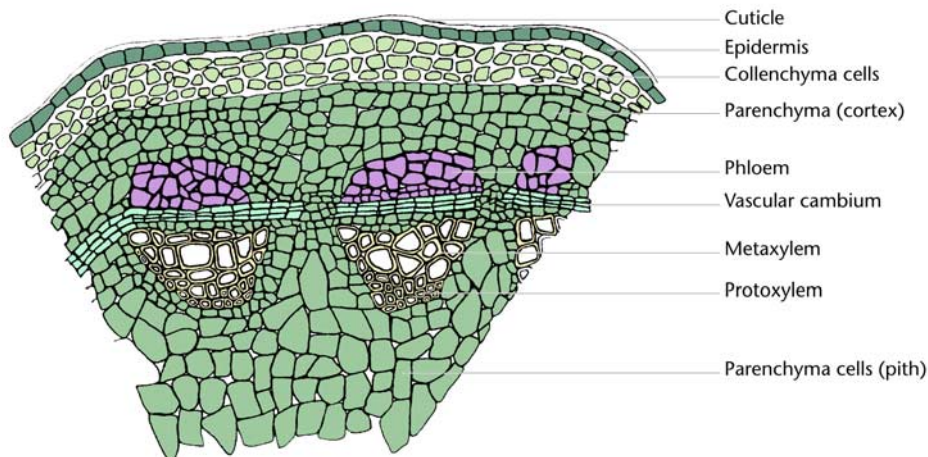


Figure 2 Cross-section of a dicotyledonous stem.

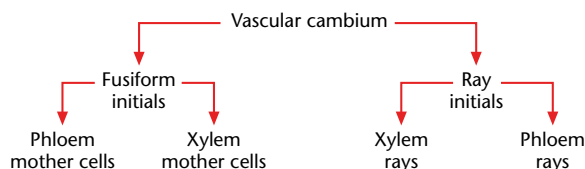


Figure 3 Production of secondary vascular tissue from the multistep meristem.

insects and herbivores. Protection may be passive (blocking access to the plant surface) or active, through secretion of toxins.

Trichomes of the stinging nettle have brittle silica tips that readily break off to inject grazing animals or passing hikers with irritating histamines. The most elaborate trichomes are perhaps those on the leaves of the insectivorous sundew (*Drosera*). These excrete a sticky nectar to attract and hold insects, then bend over in concert with leaf-folding to trap them, excrete digestive enzymes, and finally absorb nutrients from their prey.

The shoot epidermis protects the plant from desiccation, while the root epidermis allows the plant to extract water and ions from the soil, aided by their root hairs, which are trichomes. While root epidermis has a thin cuticle, its waxes have shorter chains, so it is more permeable than shoot epidermis.

Plants in secondary growth can replace their epidermis with a more substantial and complex tissue called periderm. This usually arises just beneath the epidermis, although it may form in other areas of the stem. Periderm consists of layers of three types of cell: a middle layer of phellogen (cork cambium, a lateral meristem) that produces an outer layer of phellem (cork cells) and an inner layer of phelloderm (which contributes to the cortex).

Cork cells are dead at maturity and their walls are layered with suberin and sometimes lignin, giving them great resilience to desiccation and insect or pathogen attack. Periderm also develops in roots, but there it usually arises from the pericycle, which is just outside the phloem.

Gaps occur in the phellem called lenticels, which arise under stomata in the epidermis and persist as blisters in tree bark. They allow gas exchange with the underlying tissues that the periderm so well protects. Unfortunately, they provide a constantly open route for infection and herbivory.

‘Bark’ generally means all of the tissues outside the vascular cambium (secondary phloem, phloem fibres, cortex, and the periderm). Bark has many different patterns because periderm forms at different rates at different places on the stem. Also, the cork breaks apart as the stem expands in circumference. New cambia arise under other ones, pushing the old periderms out.

Protective cell layers occur in roots, stems, and sometimes leaves. The most prominent such layer is the endodermis, commonly found in roots. It forms the innermost cell layer of the cortex, separating it from the stele (vascular cylinder). The endodermal cell wall contains suberin, which is usually restricted to a narrow, thin strip called a Casparian band that runs around the middle of each cell in its radial and tangential walls. Endodermal cells are often extensively lignified, forming characteristic U-shaped (‘phi’) thickenings that arch half-way around each cell to meet the Casparian bands.

The Casparian band effectively prevents uncontrolled entry of water and ions, absorbed from the soil, into the stele through the apoplast (the cell walls and intercellular spaces). The Casparian band directs transport through the cytoplasm of the endodermal cell, which subjects it to

physiological influence, allowing selective uptake by the plant.

An endodermis may occur in the stem, where it usually lacks a Casparian band or phi thickening. Special staining methods are needed to make it visible. Stem endodermis is sometimes referred to as a starch sheath, but since the starch itself may be absent, the term is not useful. Some aquatic plants do have an obvious endodermis in their stems and in their leaves as well.

An exodermis (or hypodermis) forms the outermost layer of the cortex, directly beneath the epidermis. It is often more obvious in monocotyledonous plants than in dicotyledonous plants. It can be lignified and can have a Casparian band. Normally a feature of stems and roots, the needle-like xerophytic leaves of conifers have a prominent exodermis and endodermis.

Ground Tissues

Parenchyma, composed of undifferentiated, isodiametric cells, with thin cell walls, large vacuoles, and thin parietal cytoplasm, occupies much of the cortex and pith of stems and roots. In roots, parenchyma often has a storage function, and stem parenchyma contributes support if it is turgid. The swollen protoplast of each cell presses outwards against the cell wall, and all of the parenchyma cells together press out against the restraining layer of collenchyma and epidermis of the outer stem. It is believed that pressure in the pith parenchyma contributes to stem growth.

Collenchyma, a living tissue with primary cell walls that are unevenly thickened, provides support to seedlings and growing stems. It occurs in the cortex just beneath the epidermis of the stem and in the midribs of dicotyledonous plant leaves. It is rare in dicotyledonous plant roots, and comparatively uncommon in monocotyledonous plants. Sometimes collenchyma is photosynthetic.

Collenchyma can grow with the plant and allow it to bend without breaking, providing plastic support, features made possible by the relatively high hemicellulose content of collenchyma cell walls. It supports the plant only if it is not under water stress, because its cell walls contain no lignin or other hydrophobic component. Thus it does not prevent wilting.

Sclerenchyma provides more robust support. Its cells have thick lignified secondary walls, which make it both strong and waterproof. This tissue helps prevent wilting, but it is expensive in terms of energy and metabolites for the plant to make. It is a more permanent tissue than collenchyma and provides elastic support to maintain the established shape of the plant.

Sclerenchyma is widely distributed, occurring as a bundle cap outside the phloem in vascular bundles, and as a bundle sheath (common in monocotyledonous plants).

The bundle cap physically protects the inner tissues of the stem. In grass leaves, the bundle sheath may extend to the epidermis, forming a bundle sheath extension. Sclerenchyma cells only become mature when the surrounding cells stop growing. They are usually dead at maturity, although the lumens of the cells remain connected by pits.

Sclerenchyma cells occur in two forms: fibres, which are long (up to 55 cm in the case of hemp fibres) with tapered ends, and sclereids, which are more or less isodiametric. Brachysclereids, or stone cells, form in clumps in the flesh (mesocarp) of the Bartlett pear (*Pyrus communis*), giving it a characteristic grittiness. They form a dense layer to make the endocarp ('shell') of the coconut. Many seed coats (testas), especially those of legumes, are made of a double layer of sclereids.

Branched astrosclereids occur in the petioles and blades of water lily leaves (*Nymphaea*), making them leathery and resistant to the tearing forces of waves and currents.

Some botanists distinguish between support sclerenchyma (fibres and sclereids) and conducting sclerenchyma (vessels and tracheids). Xylem vessels provide both support and transport capabilities, but one function comes at the expense of the other because thicker walls reduce their internal diameter.

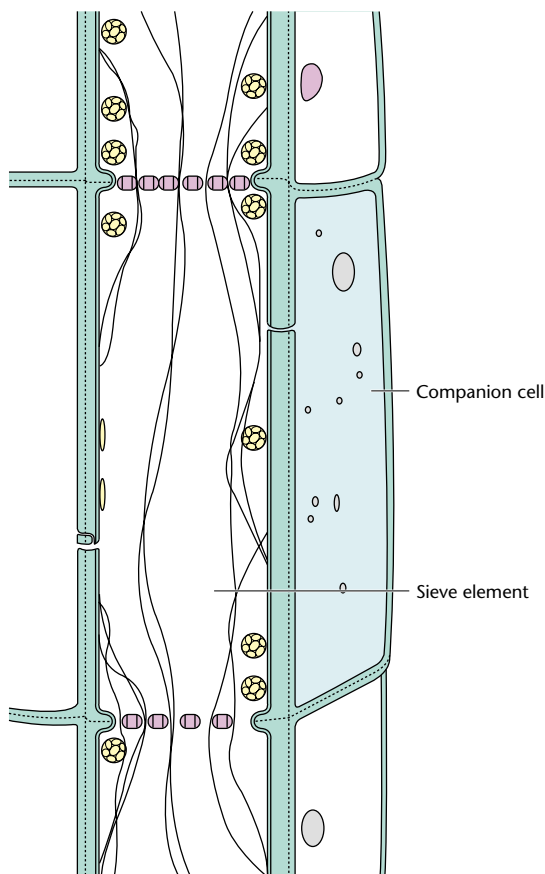
Vascular Tissues

Higher plants have two transport systems, the xylem and the phloem, which comprise their vascular tissue. They have somewhat different functions, but generally arise together and are nearly always found running side by side within all organs of the plant.

Xylem transports water and various dissolved ions from the roots upward through the plant. Phloem transports a solution of metabolites (mainly sugars, amino acids, and some ions) from 'sources' of production, such as fully expanded leaves, to 'sinks,' such as developing leaves, fruits, and roots. Both tissues contain long tubular cells (and some other associated cells) joined end to end that are responsible for transport.

Phloem is predominantly a living tissue, consisting of sieve tubes, companion cells (**Figure 4a**), phloem parenchyma, and phloem fibres. Each sieve tube consists of a file of sieve elements, called sieve tube members in angiosperms. Sieve element is the collective term for the sieve tube members, in most angiosperms and the sieve cells in non-angiosperms. But this discussion will not deal with the somewhat different, and much less understood sieve cell, so the term 'sieve element' is used here in place of the wordy 'sieve tube member'.

Sieve elements are joined by thick end walls, called sieve plates, which are pierced by large, modified plasmodesmata (cytoplasmic bridges between cells) called sieve pores. Sieve pores are lined with the complex carbohydrate



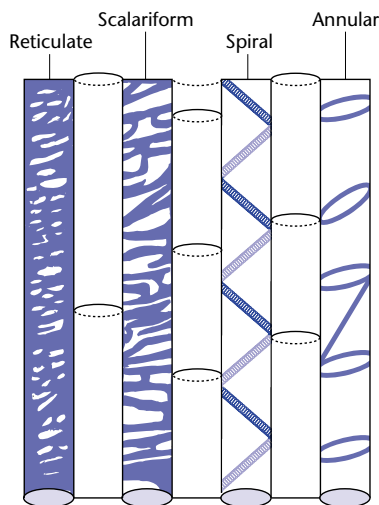
(a)

Figure 4 (a) Sieve tube and companion cells.

callose, which rapidly proliferates to seal the pores in response to damage to the phloem such as that caused by grazing animals. Sieve elements contain only a little cytoplasm, dominated by amyloplasts (starch-filled plastids) and filamentous proteins. When mature, they lack a nucleus and tonoplast, but retain a plasmalemma, indicating that they are living cells. Sieve elements have thick primary cell walls through which pass abundant plasmodesmata, connecting them to small companion cells that cluster around each sieve element.

Companion cells contain large nuclei, dense cytoplasm with abundant organelles (especially mitochondria), and many small vacuoles. These features are related to the functional association of companion cells and elements.

Xylem is mostly a dead tissue, consisting of vessels, tracheids, xylem parenchyma and fibres. The conducting cells of the xylem, the tracheary elements, are the vessels and tracheids. These are dead at maturity, and have



(b)

Figure 4 (b) Xylem vessels.

secondary walls crosslinked with the complex polymer lignin. Various patterns of lignin deposition occur, ranging from annular, helical, scalariform, reticulate, to pitted (**Figure 4b**), depending on the age of the cell. As the degree of lignification increases, the resistance to water stress increases.

Vessels consist of cylindrical vessel elements (also called vessel members) joined together by large openings in their end walls called simple perforation plates, ridges representing the remnants of degraded end walls.

Although transport can occur freely through the perforation plates of vessels, movement also takes place laterally, among adjacent vessels, and with adjoining xylem parenchyma cells. This happens across areas of primary wall where no secondary wall has been deposited. Vessels with annular thickenings provide the greatest area for lateral transport, with less area becoming available as the degree of lignification increases.

Lateral transport in pitted vessels is restricted to structures called pits. These occur as two main types, simple pits and bordered pits. Simple pits are areas of bare primary wall in vessels otherwise covered with lignin. Bordered pits contain pressure-sensitive valves that prevent air embolisms from interrupting flow between cells.

The other type of tracheary element is the tracheid, which has a thin secondary wall, tapered ends, and no perforation plates. It is connected to adjoining cells only by pits. While tracheids are found in both gymnosperms and angiosperms, only the most advanced gymnosperms contain vessels.

The Organ System

Root

Roots anchor plants in the soil, absorb water and ions from it, produce plant growth regulators, and store sugars and starch. Structurally, roots have four external zones, beginning at the tip with the root cap, which protects the root apical meristem and secretes mucigel. This absorbs water from the soil to facilitate ion diffusion into the root, fosters growth of bacteria that release more nutrients, and lubricates the root to ease passage through the soil. Behind the root cap is the elongation zone, where cells elongate to add length to the root. This is followed by the root hair zone. Root hairs are short-lived (one or two days), fragile, outgrowths of epidermal cells that greatly increase the volume of soil that can be mined by a plant for nutrients. Last is the lateral root zone or maturation zone, characterized internally by the presence of an endodermis that encloses the stele (pericycle and vascular tissue) (Figure 5).

Root growth is indeterminate and is governed by the moisture, fertility, composition and homogeneity of the soil, such that growth occurs in patches, making root architecture variable. In general, a seedling produces a primary root that grows straight down and gives rise to secondary lateral roots. These may produce tertiary roots,

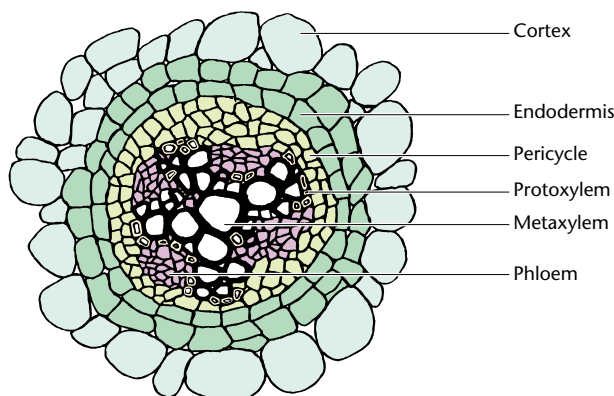
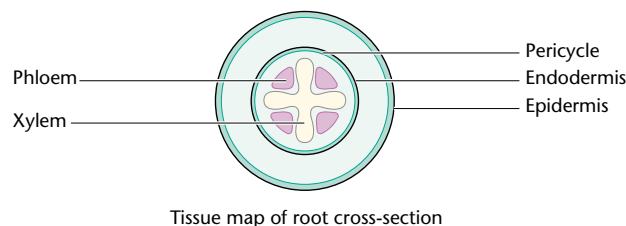


Figure 5 Root cross-section.

which in turn may branch, with the process continuing almost indefinitely. New roots arise endogenously from the pericycle of the main root. Lateral roots may exist as primordia in the embryo before germination, where they are called seminal roots.

Root modifications

Tap roots, like that of the carrot (*Daucus carota* L.), are modified for storage (Figure 6a). Another storage root is the root tuber, which is really a swollen adventitious root (sweet potato, *Ipomea batatas* L.)

Aerial roots occur on epiphytic orchids, and have a multiseriate epidermis called velamen made of dead cells with suberized walls. Velamen apparently absorbs water and nutrients during wet conditions and retains water during dry conditions. Some aerial roots are photosynthetic.

Pneumatophores (breathing roots) occur on some mangrove trees. They grow upwards through the substrate, usually anaerobic mud, and bear lenticels that allow gas exchange when exposed at low tide.

Prop roots are a type of adventitious root. They provide more transport capability to monocotyledonous plants as well as extra support. They arise from the lowest nodes and grow downwards through the air to the soil. Once there they may contract slightly to help anchor the plant (maize, *Zea mays*; screw pine, *Pandanus veichii*).

Contractile roots shrink even more than prop roots, and pull growing corms, bulbs and rhizomes down in the stable soil environment, hiding them from herbivores (ginger, *Zingiber officinale*; dandelion, *Taraxacum officinalis*) (Figure 6b and c)

Root nodules, found mostly on legumes, harbour *Rhizobium* bacteria, which receive nutrients from the host plant and in return fix N_2 gas to NO_3 for the host to use.

Parasitic plants have haustorial roots that invade the cortex and vascular tissue of the host plant. Some rely partly (birdvine, *Phytora stelis*), others more completely (dodder, *Cuscuta*), on the host for food, depending on whether or not they invade the phloem.

Stem

The stem and its branches allow leaves to be arranged to maximize exposure to sunlight, and flowers to be arranged to best attract pollinators. Branching arises from the activity of apical and axillary buds. While branching is a complex topic, four basic patterns can be identified.

Monopodial plants have a rhythmically active shoot apical meristem, with axillary shoots that remain secondary and regulated by the main shoot apex. Most conifers exhibit monopodial branching.

In plants with sympodial branching the shoot apex becomes reproductive or aborts. One axillary shoot grows upward and becomes the main stem. Its shoot apex

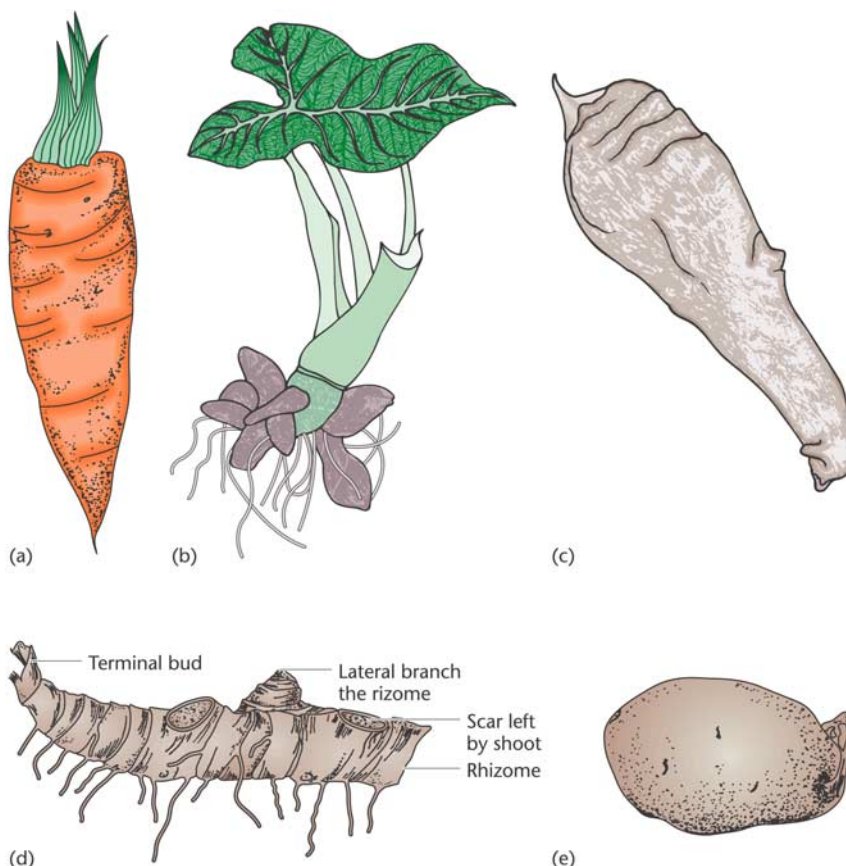


Figure 6 (a) Carrot, modified tap root. (b) Tanna, plant. (c) Tanna, corm. (d) Ginger, rhizome. (e) Potato, stem tuber.

becomes reproductive or aborts, and so on. The characteristic pagoda shape of the seaside almond (*Terminalia catapa*) results in part from this growth habit.

In dichasial (or dichotomous) branching the terminal bud splits into two buds on opposite sides of the stem. These grow at a similar rate and then branch again, resulting in a repeatedly forked appearance. Many plants display superficial dichasial branching, but only some palms and cacti exhibit true dichasial branching.

Although shoots usually arise from apical or axillary buds, they may appear endogenously from any organ, creating adventitious branches. Sweet potato (*Ipomea batatas*) owes its scrambling habit to stems arising from the roots, giving the plant a disorganized appearance.

Stem modifications

Stems serve other functions besides or instead of support. Some are modified for storage. Bulbs consist of flattened, short stems with thick, fleshy nonphotosynthetic storage leaves (onion, *Allium cepa*). Corms are vertical, enlarged fleshy stem bases with scale leaves (dasheen, *Colocasia*

esculenta; *Gladiolus*), while rhizomes (**Figure 6d**) are fleshy horizontal stems, also with scale leaves (arrowroot, *Maranta arundinacea*; ginger, *Zingiber officinale*). Stem tubers are thick storage stems, usually horizontal (yam, *Dioscorea*; Irish potato, *Solanum tuberosum*) (**Figure 6e**).

All of these are both underground storage stems, and organs of perennation, enabling plants to survive periods of drought or cold, storing food reserves away from most herbivores, in a relatively stable environment. The stem of sugar cane (*Saccharum*) is an aerial stem tuber. Storage stems are propagative, and will produce new shoots and roots.

Stolons (which bear foliage leaves) and runners (which have only scale leaves) allow plants to spread vegetatively above ground. These are indeterminate propagative stems with long, thin internodes that readily root at the tip to form new plants if growing conditions are favourable (*Paspalum* sp., saxifrage, spider plant). They have no storage or support function.

Although many stems photosynthesize to augment their leaves, some stems are more specifically designed to replace them. The cladode is flattened to look vaguely leaf-like

(prickly pear cactus, *Opuntia*), but it is swollen for water storage (succulent), too. The conifer-like needles found on the she oak (*Casaurina*) are better examples of photosynthetic stems. They are not enlarged for storing anything, and they have tiny, vestigial leaves.

Some stems provide support by wrapping around another plant or other support. Many members of the Convolvulaceae are vines, and they have twining stems that wrap especially well round wire fences.

Leaf

Leaves are designed to provide plants with photosynthates, but they are modified to provide protection (spines, bud scales), support (tendrils), storage (onion bulb), nitrogen acquisition (insect trap leaves), and pollinators (flower petals). Typical dicotyledonous plant leaves have a large surface area to maximize photosynthesis and a thin profile to expose lots of chlorophyll to the light. At the same time they must dissipate wind forces and heat, retain water, allow gas exchange for photosynthesis and respiration, and exclude pathogens.

By extending the leaf blade (lamina) away from the stem by a flexible leaf stalk (petiole), shading from the stem is reduced and the leaf can flutter. Fluttering promotes cooling, decreases insect and pathogen attack, dissipates wind forces to reduce damage, and increases carbon dioxide absorption. Monocotyledonous leaves are usually narrow and belt-shaped, with a sheathing base, and they move easily in the wind, too.

The upper epidermis of most dicotyledonous plant leaves has a thicker cuticle and fewer stomata than the lower epidermis, and palisade mesophyll cells, the major sites of photosynthesis, are arranged above spongy

mesophyll, where gas exchange occurs (Figure 7). The dorsal and ventral surfaces of many monocotyledonous leaves are more or less the same and their internal tissues are more homogeneous than stratified.

Leaf modifications

Spines consist entirely of compact bundles of sclerenchyma fibres. They can, if densely packed, shield the plant against intense sunlight and the drying effect of wind. Thorns are, to some botanists, simply spines that may contain vascular tissue and are modified stems, not leaves (Figure 8a). Both arise from axillary buds and provide protection from herbivores.

Tendrils lack a blade, like spines, but photosynthesize, never stop growing, and help support the plant (Figure 8b). They are touch-sensitive, not light-sensitive, and coil around things, especially stems of other plants. Coiling results from growth occurring faster on the outer side of the tendril away from the inner side in contact with the support. Tendrils are commonly found in many plants including Cucurbitaceae (cucumber, melon), Passifloraceae (passion fruit) and the Convolvulaceae. Both spines and tendrils can be modified stems, not leaves. Indeed, spines arise from adventitious roots on a species of mangrove, and some tendrils even arise from inflorescences.

Sclerophyllous leaves are xerophytic, designed to withstand a desert-like environment. Like spines, they have abundant fibres but retain photosynthetic ability. Such leaves are expensive for the plant to make and so tend to be long-lived. Ordinary leaves, by contrast, are cheap and mass-produced by many plants, and are expendable. Sclerophyllous leaves are especially common among the monocotyledonous plants, for example, *Agave sisalana*. The fibres that make leaves of this plant so durable are used to make sisal rope.

Succulent leaves are also xerophytic, with few air spaces and a thick cuticle (Figure 8c). The mesophyll is isolated from the leaf surface by cells with large vacuoles, which filter heat from intense sunlight. Succulent leaves often contain mucilage, which binds water so it can be stored in the leaf. The vascular tissue is 'conserved'. There is not much of it because little transport occurs in these leaves. *Aloe vera* is a good example. Both succulent and sclerophyllous leaves have a small surface area to volume ratio, reducing transpiration losses.

Bud scales (cataphylls) are tough, sessile (lacking a petiole), nonphotosynthetic leaves (actually stipules) that protect apical or axillary buds, during dormancy, against herbivores and drying winds. Common on temperate trees, in the tropics they are found on the Para rubber tree (*Hevea brasiliensis*), *Magnolia* and mahogany (*Sweetinia macrophylla*). They often form cork cambium that makes a thin bark, the only type of leaf to do so.

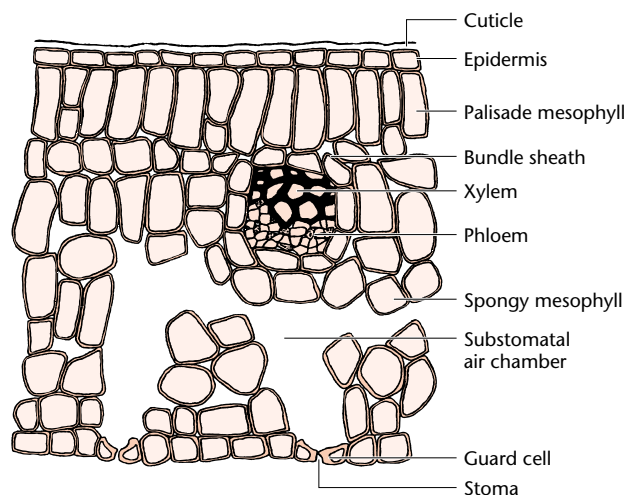


Figure 7 Transverse section of a leaf.

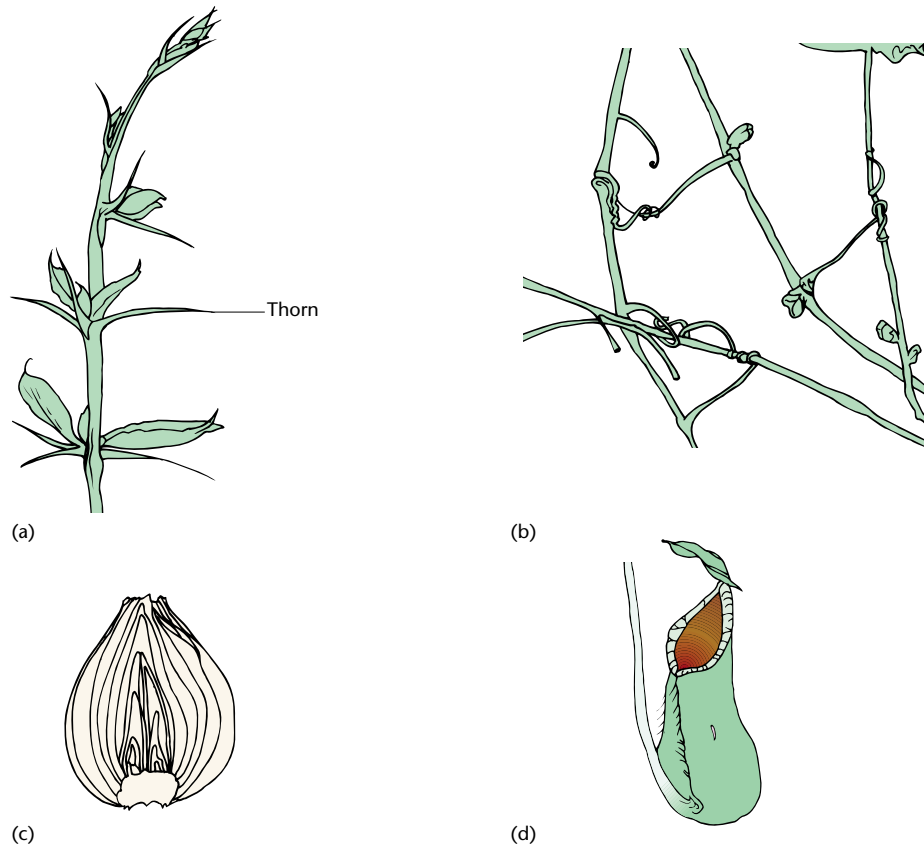


Figure 8 Modified leaves. (a) Barberry thorns. (b) *Vitis vinifera* tendrils. (c) Onion – succulent leaves, bulb. (d) *Nepenthes* sp. – lamina of each leaf is modified into a pitcher-shaped chamber.

Trap leaves are found on insectivorous plants, which tolerate nitrogen poor soil by trapping and digesting insects. The highly modified pitchers of pitcher plants (*Nepenthes*, *Sarracenia*, *Darlingtonia*) are typically red brown, like carrion, and lined with glands that release digestive enzymes. They may have lids to exclude rain, downward-pointing trichomes, and abundant flaky wax to prevent the escape of insects. In *Nepenthes* (Figure 8d) the petiole of the trap is elongate, wide, and flat, like a normal lamina, forming a phyllode. This structure compensates for the reduced photosynthetic role of the pitcher. Other kinds of trap leaves occur on the Venus flytrap (*Dionaea*), sundew (*Drosera*) and bladderwort (*Utricularia*).

Flower

A flower is a shoot system consisting of a determinate axis with laterally borne, concentric rings of four kinds of leaves designed for sexual reproduction: sepals, petals, stamens and carpels (Figure 9). Green sepals closely resemble leaves,

while petals and coloured (petaloid) sepals have a poorly developed vascular system, no palisade mesophyll, little sclerenchyma, and chromoplasts instead of chloroplasts. Most stamens and carpels do not look like leaves, but in the more primitive flowers (*Drimys*, *Magnolia*, *Michelia*), they may be wide and flattened, pointing to their origin.

Because petals and sepals are not necessary for reproduction they are accessory parts, while stamens and carpels are essential parts. The sepals together form the calyx of the flower, and the petals together make up the corolla, with both whorls together comprising the perianth. The stamens (filament + anther) are the male parts (androecium), and the carpels (ovary + style + stigma) are the female parts (gynoecium).

Flowers arise in the axils of leaves. These leaves, which are usually small, are called bracts. Some flowers have conspicuously coloured bracts that supplement the petals or even replace them (*Poinsettia*, *Bougainvillea*). A stem bearing a single flower is a pedicel, and the point of attachment of the flower to the pedicel is the receptacle. The stem of an inflorescence, a branched system of flowers, is a peduncle.

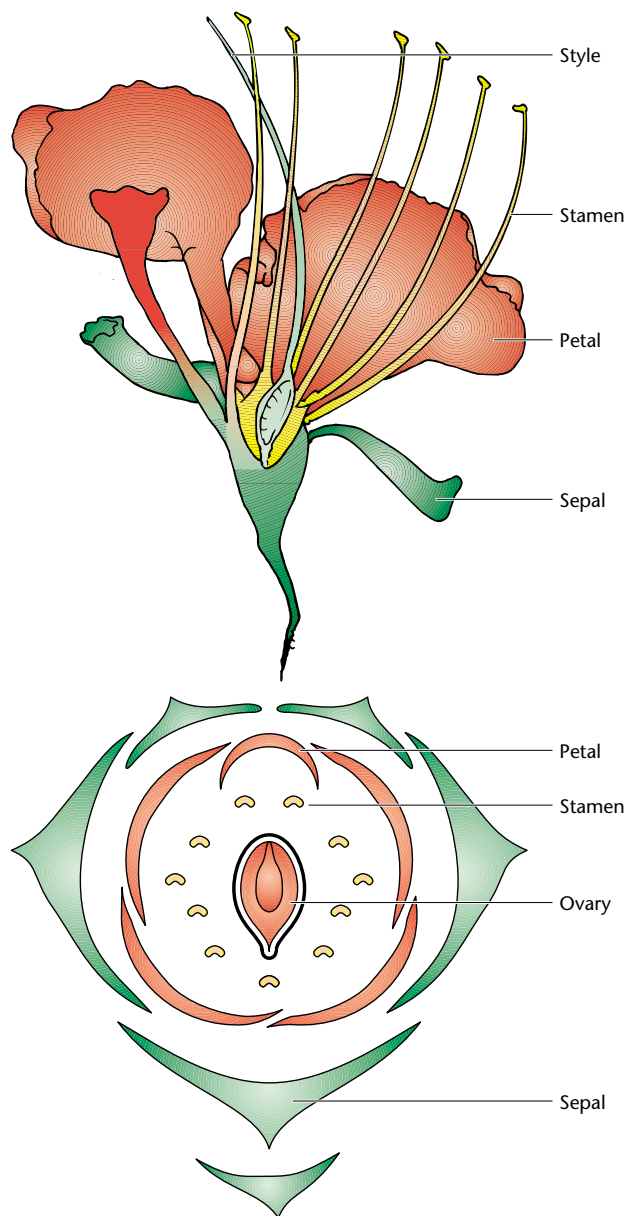


Figure 9 Barbados Pride (*Caesalpinia pulcherrina*).

Floral modifications

Loss of parts

A complete flower possesses all four whorls; an incomplete flower lacks one or more of them. A perfect or hermaphrodite flower has both carpels and stamens, but may lack sepals, or petals, or both. An imperfect flower lacks either carpels or stamens. A staminate (male) flower has only stamens, no carpels; a carpellate (female) flower has only carpels.

On a maize plant, the ear is a carpellate imperfect inflorescence. Its silks are greatly elongated styles, with sticky stigmatic surfaces for catching airborne pollen. The tassel is a staminate imperfect inflorescence. Maize is monoecious because it has both male and female flowers on the same plant. Most cucurbits are monoecious too. Papaya (*Carica papaya*) is dioecious, with male and female flowers borne on different plants.

Fusion of parts

Within whorls, if the sepals are fused to form a tube, the flower is gamosepalous (*Hibiscus*). If the petals are fused, it is gamopetalous (*Allamanda*). If the petals are free (no fusion) it is polypetalous. The usual fusion between whorls is between stamens and sepals; such stamens are adnate to the petals, producing an epipetalous flower.

If the filaments of the stamens are fused into a tube, they are connate, and the androecium is adelphous. If the carpels are fused, the gynoecium is syncarpous, and if they are free, it is apocarpous. Fusion of gynoecium and androecium produces a gynostegium. Many legumes (of the Papilionoideae) and all Compositae have their stamens fused to form a tube.

Ovary structure

Ovules arise from swellings on the inside of the ovary wall called placentas. A simple ovary, with one carpel, has marginal placentation, with the ovules arising along the junction of the two margins of the carpel. If there is more than one carpel, the placentation becomes parietal. If the ovules are attached to the central axis formed by the carpels, it is axile. In central placentation, there is only one locule, and the ovules are borne on a central axis, and in free central placentation the axis is incomplete. In basal placentation there is also one locule, and the ovules are attached to the base of the ovary.

Ovary position

Flowers that are hypogynous, meaning that the other flower parts are 'below the gynoecium', have convex receptacles (Figure 10). The ovary is superior to the rest of the flower. A perigynous ('around the gynoecium') flower has a concave receptacle, so the ovary is below the other floral parts, and is half superior. In epigynous ('above the gynoecium') flowers the ovary is inferior and embedded in the receptacle.

Aestivation

Flowers show variation in the horizontal arrangement of their calyx and corolla (aestivation). In a valvate flower, the petals or sepals meet without overlapping. In a contorted or regular flower, the petals or sepals all overlap in the same direction. In an imbricate or irregular flower, the petals or sepals overlap in both directions, so that one sepal or petal

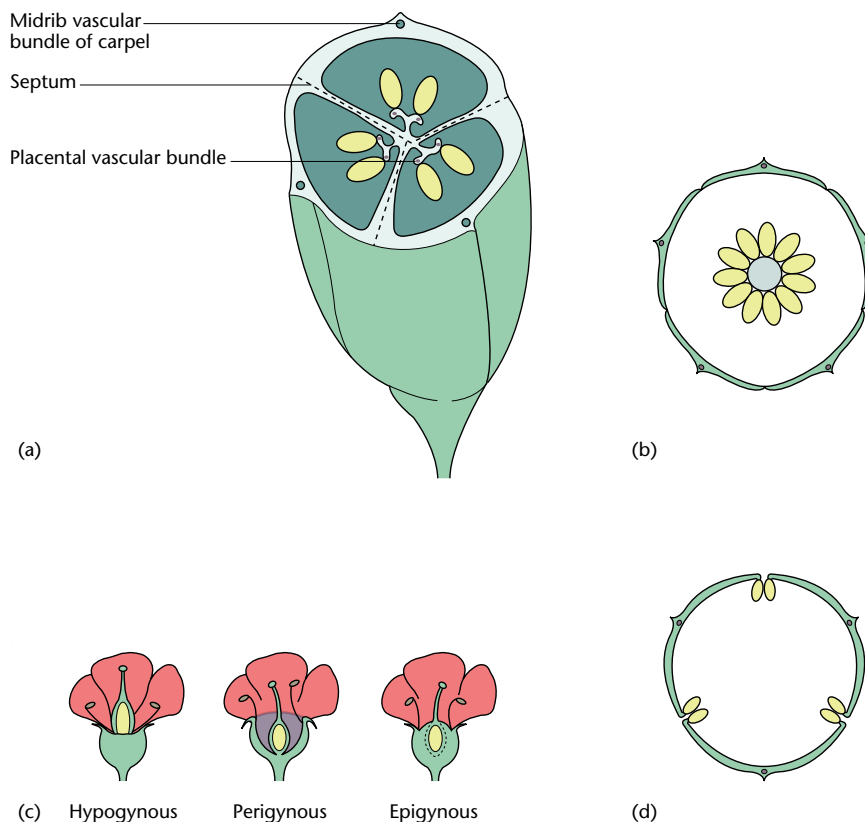


Figure 10 Ovary structure and position in flowers. (a) Transverse section of a trilobular trilocarpellary ovary. (b) Unilocular ovary. (c) Ovary position. (d) Unilocular trilocarpellary ovary.

is wholly inside the ring, and at least one other is wholly outside the ring.

Floral shape

Actinomorphic flowers exhibit radial (multilateral) symmetry. All the floral parts in each whorl are alike in size and shape, and any longitudinal cut across the centre creates two mirror image halves (*Hibiscus*, *Cucurbita*). Zygomorphic flowers have bilateral symmetry, and only one specific longitudinal cut across them will produce mirror image halves. This symmetry results from differences in the size and shape, or loss, of some of the parts (Orchidaceae, Leguminosae). In asymmetric flowers there is no symmetry to the arrangement of the parts (*Canna*).

Fruit

Fruits are, to a botanist, different from what may be construed from the popular notion of 'fruits and vegetables'. The green bean (*Phaseolus vulgaris*) is a fruit, not a 'vegetable', the coconut is not a nut (although both

coconuts and nuts are fruits), and the banana is an example of a berry.

A true fruit is the mature ovary of an angiosperm. The maturation of the ovule(s) to form the seed(s) within the ovary is normally accompanied by a thickening of the ovary wall to form three layers that comprise the pericarp. The outer layer (exocarp) may simply be a layer of epidermis, as in the grape, the middle layer (mesocarp) is commonly soft, like the flesh of the mango, and the inner layer (endocarp) can vary from gelatinous (tomato) to stony (the 'pit' or 'stone' of the peach) (Figure 11).

In general, fruits may be classified according to four criteria:

- The number of flowers involved in their formation.
- The number of ovaries.
- The degree of hardness of the mesocarp – dry and hard or soft and fleshy.
- The ability of the fruit to dehisce (split open when mature) or not.

See **Table 1** for a classification of fruits.

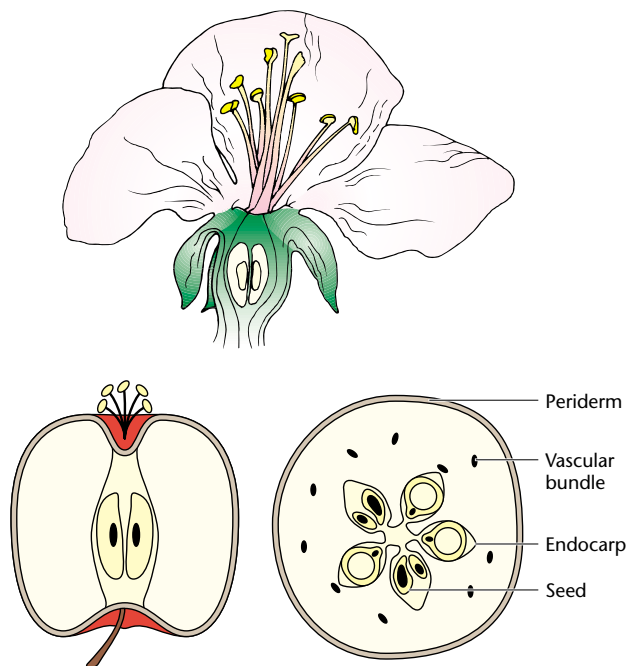


Figure 11 Apple flower and fruit structure.

Seed

The seed is the mature, fertilized ovule of a flower. It contains an embryonic plant in a resting state before initiation of germination, and a food store. An enveloping seed coat (testa), which is derived from the integument cell layer(s) within the nucellus (megasporangium), provides protection. A pore remains at the apex, the micropyle, through which the pollen tube reaches the ovule. Beside the micropyle is the hilum, a scar created when the seed breaks free of the seed stalk (funiculus). Seeds that store food are albuminous seeds, those that do not are exalbuminous seeds. Food stores (carbohydrates, proteins, lipids), can be endospermous (derived from the large central cell of the nucellus, perispermous (proliferated nucellus tissue), or both.

Embryos of many dicotyledonous plant seeds absorb their food stores well before germination, with notable exceptions, for example castor bean, *Ricinus communis*, which has oily seeds. On the other hand, many monocot seeds retain a prominent endosperm, like the grasses wheat, oats, barley, rice, and corn. The grass embryo has a large scutellum, which excretes enzymes to digest the endosperm and provide the embryo with food.

Seed dispersal

Reproductive success is very much enhanced if seeds are distributed to new habitats. To this end seeds and their associated fruits show a variety of adaptations to take advantage of various vectors of dispersal (Figure 12).

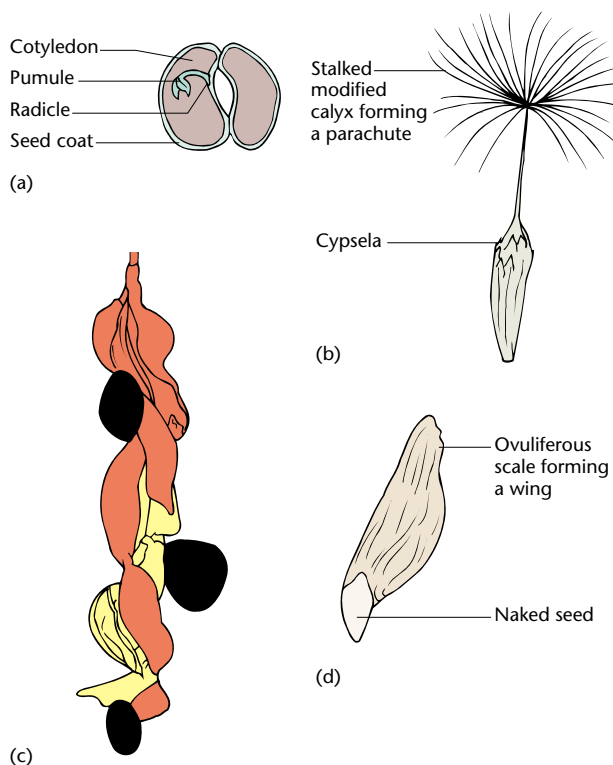


Figure 12 Seed dispersal modifications. (a) Representation of a dicotyledonous seed. (b) Dandelion. (c) Legume, *Pithecellobium arboreum*. (d) Pine seed.

Animals

Many berries have attractive and edible pericarps, with small, slippery seeds that are protected by hard woody testas, well suited to being consumed and surviving digestion. While the testa of drupe is thin, the woody endocarp protects the seed, making it suitable for ingestion. Arils, which are normally fleshy accessory outgrowths, usually of the funiculus, facilitate the dispersal by animals of seeds of the akee (*Blighia sapida*, monkey pot tree (*Lecythis ollaria*)). They also appear on the seeds of better-known fruit like tomatoes. Testas and pericarps may have spines, burrs, or other outgrowths designed to engage animal fur or hikers' socks as the vector of dispersal.

Water

The coconut fruit is buoyant and seaworthy because of the air held in its hollow seed, which is protected by a tough endocarp made of sclereids, and by the air in its fibrous mesocarp, which in turn is protected by a tough, waxy exocarp. Growth of the beached, germinating seed is aided by rainwater retained by the mesocarp. Seeds of the red mangrove (*Rhizophorus mangle*) are viviparous, with no dormant period. They produce leaves and a prominent

Table 1 A Classification of Fruits

Simple fruit. Fruit derived from a solitary carpel in a single flower

A. *Dry fruits*: having a mesocarp that is definitely dry at maturity

(i) Indehiscent fruits

(a) Arising from one carpel

Achene – small, with seed single attached at one point to a thin pericarp (sunflower, *Helianthus*).

Cypsella – similar to achene, but arises from an inferior ovary (Compositae), making it a false fruit.

Caryopsis – also called grain – similar to an achene, but pericarp and testa of single seed are fused (all grasses).

Samara – Testa modified into a wing-like structure, may be one-seeded (elm, *Ulmus*) or two (maple, *Acer*).

(b) Arising from a compound gynoecium with several carpels

Nut – Ovary has several carpels, all but one atrophy. One seeded, with woody pericarp of sclereids (walnut, *Juglans*)

(ii) Dehiscent fruits

(a) Arising from one carpel

Follicle – pod-like fruit, splits open on one side (milkweed, *Asclepias*, cotton, *Gossypium*).

Legume – breaks open on both sides (all beans, peas of the Leguminosae).

(b) Arising from a compound gynoecium with many carpels

Silique – two sides split, seeds remain attached to a false central partition or replum (Brassicaceae). The silique (mustard, *Brassica*) differs from the siliqua (or silicle), which has a length less than twice its width (shepherd's purse, *Capsella*).

Capsule – carpels split apart in different ways (mahogany, iris, lily, poppy; akee, *Blighia sapida*, may be considered a fleshy capsule).

(iii) Schizocarpic fruits: Arising from a compound ovary; the locules split into separate (usually dry) fruits

Schizocarpic mericarp – twin mericarpic fruits joined at one point (parsley family)

B. *Fleshy fruits*: Having a mesocarp that is soft at maturity

Berry – (true berry or bacca) - endocarp, mesocarp, and exocarp all soft and easily distinguishable (blueberry, *Vaccinium vacillans*; tomato, *Solanum*)

Drupe – similar to a berry, but endocarp is woody (mango, *Mangifera indica*; peach, *Prunus persica*).

Pome – (also classed as a false fruit) – similar to drupe, except with papery endocarp (apple, *Pyrus malus*).

Pepo – similar to berry, but with a thick, tough exocarp. May also be classed as false fruits (pumpkin, squash, all Cucurbitaceae).

Hesperidium – leathery exocarp with oil glands (all citrus).

continued

Table 1 *continued*

Aggregate fruits. Formed from one flower with many ovaries maturing together, some types fusing with receptacle

Etaerio – consists of an aggregate of achenes, berries, or drupes (Raspberry, *Rubus*; strawberry, *Fragaria* – also classed as a pseudocarp, a kind of false fruit).

Multiple fruits. Developing from the ovaries of several flowers of an inflorescence which mature together.

(a) Fleshy Multiple Fruits (May also be classed as accessory fruits)

Sorosis – fruits on a common axis and derived from the ovaries of several flowers that are usually coalesced (mulberry, *Morus*; pineapple, *Ananas comosus*; breadnut, *Artocarpus atilis*).

Syconium – a syncarp with achenes attached to the inside of an infolded receptacle (*Ficus*).

(b) Dry Multiple Fruits

Strobilus – multiple fruit of achenes including bracts (hop, *Humulus lupulus*).

Accessory / False fruits. The ovary wall can be augmented by various tissues that protect the seeds, including the receptacle of soursop, the perianth of breadnut, and the scaly bracts of pineapple. Fruits that develop from inferior ovaries are false fruits. In an apple the mesocarp and receptacle merge together with no exocarp discernible, because the carpels become fused to the accessory tissue during fruit ontogeny. In the flesh of the apple two sets of vascular bundles, one previously leading to sepals, the other to petals before the apple formed, remain visible. The true fruits of a strawberry are the tiny yellow or brown ‘seeds’, which are really achenes, on the surface of the swollen red receptacle.

torpedo-shaped root while still attached to the parent tree, and seedlings eventually break free to be carried away by the tide.

Wind

Seeds dispersed by the wind must be small and light and produced in great numbers to reach suitable habitats. To this end, some orchids produce dust-like seeds by the million, their mass measured in nanograms. Milkweed seeds have plumes, really extended dead trichomes, which equip them for dispersal. The dandelion seed is really a cypsela fruit, and its plume is a pappus, a modified calyx. The mahogany fruit, a type of capsule, splits open when mature to release its seeds, which have winged testas, so they can rotate and float away from the parent tree.

Self-dispersal

The pericarps of some legumes split open explosively to release their seeds (purple vetch, *Vicia benghalensis*; Scotch broom, *Cytisus scoparius*). This phenomenon results from the sudden release of tension, created in the maturing pericarp by layers of fibres in the pericarp shrinking in opposite directions, when the carpels are broken apart. Hydrostatic pressure built up in the fruit of dwarf mistletoe (*Arceuthobium pusillum*) can expel seeds as far as 15 m from the parent plant.

Acknowledgements

The author would like to thank Erin Mangal for supplying the original artwork for this article.

Further Reading

- Bell AD (1991) *Plant Form*. Oxford: Oxford University Press.
- Dickison WC (2000) *Integrative Plant Anatomy*. New York: Academic Press.
- Esau K (1977) *Anatomy of Seed Plants*, 2nd edn. New York: Wiley International.
- Fahn A (1990) *Plant Anatomy*, 4th edn. Oxford: Pergamon Press.
- Mauseth JD (1998) *Botany: An Introduction to Plant Biology: Multimedia Enhanced Edition*. London: Jones and Bartlett.
- Mauseth JD (1988) *Plant Anatomy*. Menlo Park, CA: Benjamin/Cummings.
- Niklas KJ (1994) *Plant Allometry: The Scaling of Plant Form and Process*. Chicago, IL: University of Chicago Press.
- Niklas KJ (1997) *The Evolutionary Biology of Plants*. Chicago, IL: University of Chicago Press.
- Raven PH, Evert RF and Eichhorn SE (1999) *Biology of Plants*, 6th edn. New York: WH Freeman.
- Simpson BB and Ogorzaly MC (2000) *Economic Botany. Plants in Our World*, 3rd edn. New York: McGraw-Hill.