Chapter 2. **Vegetative morphology of plants**

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INTRODUCTION: THE PLANT'S BASIC BODY PLAN

Most plants are photosynthetic machines: they capture the energy contained in sunlight and transform solar radiation into chemical energy stored the form of bonds in chains of carbon molecules. Through the process of photosynthesis, light and atmospheric CO_2 are combined in the leaves of green plants to form simple carbohydrates, which are then used to build other organic molecules such as cellulose, starch, oils, waxes, proteins, or DNA. Six molecules of CO_2 (and some 72 photons of light) are needed to form one molecule of glucose:

sunlight

$$6\ CO_2 + 6\ H_2O \rightarrow C_6H_{12}O_6 + 6\ O_2$$

As a byproduct of the process, six molecules of oxygen are formed and dissipated from the leaf tissue into the atmosphere.

To achieve this remarkable feat of turning atmospheric carbon dioxide into living molecules while releasing oxygen into the earth's atmosphere, plants have evolved highly specialized organs. The light-intercepting structure *par excellence* is the **leaf**. The set of leaves in the upper aerial part of the plant form the plant's **canopy**, where the plant exchanges gases with the atmosphere and intercepts light from the sun.

But in order to work its chemical wonder up in the leaves, the plant also needs water and mineral nutrients such as phosphorus, essential for the synthesis of DNA, or nitrogen, essential for manufacturing proteins. In order to obtain these, plants have developed the **root** —a complex network of underground stem-like organs— whose role is the absorption of water and mineral nutrients from the soil, and, in doing so, anchoring the plant to the ground.

Finally, the root and the leaves are connected by the **stem** —an axis of plant tissues that includes both vascular cells and strong, lignified cells— whose role is both to support the canopy high up in the air and to transport substances between the leaves and the roots.

STEMS AND ROOTS

Modular growth

Most plants have a simple system of growth based on the repetition, or re-iteration, of plant parts. The basic plant part is formed by the **node**, the **internode**, the **leaf**, and the **axillary bud**. We will call this morphological unit the plant's **metamere**, or basic module.

The **nodes** are the point of attachment of leaves and buds onto the stem or shoot. The **internodes** are stem segments between two successive nodes. The **leaves** are flattened photosynthetic organs consisting of two main parts: (a) The **blade** (or lamina) is the flattened expanded portion of the leaf; and (b) the **petiole** is a stalk supporting the blade and attaching the leaf to the node. The **stipules** (present only in some leaves) are a pair of appendages at the base of petiole. The **axil** (from the Latin *axilla*, underarm pit) is the angle of insertion between the leaf and the stem, always harboring an **axillary bud** —an immature group of stem cells, or **meristem**— from where new growth and new branching may occur.

Like a complex house made by the repetitive laying of simple bricks on top of each other, a plant is formed by the repetition of metameres. And, like in the brick house metaphor, it is not the complexity of the modules themselves but rather the way in which these basic units interact with each other what gives the final intricacy of the plant's external architecture and general appearance.

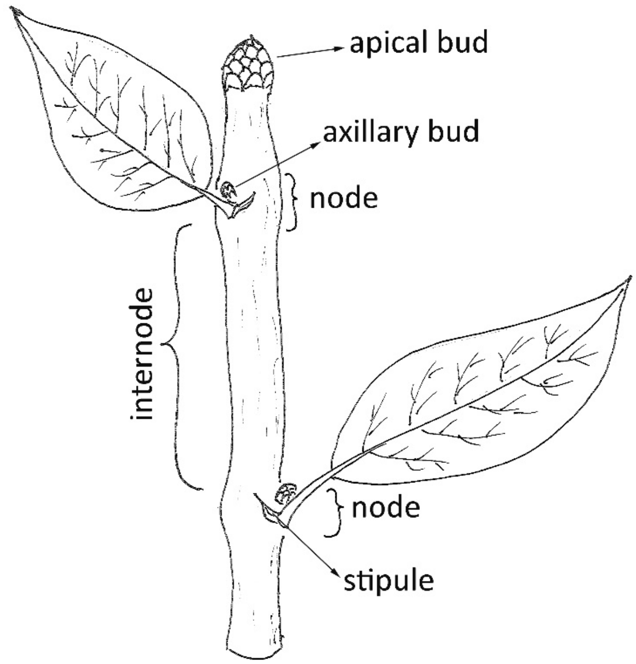


Figure 2.1. The plant metamere.

Long shoots, short shoots

One of the simplest ways through which a plant can achieve different architectural forms is by regulating the length of the internode between two successive nodes. If the internodes are long, the plant will develop a slender stalk with leaves widely separated from each other. If the internodes are short, the stem will be barely visible and a whorl of leaves will develop, tightly packed around a central axis. Short shoots are also called **rosettes**.

If a **short shoot** develops at the base of the main stem of the plant, the **whorl** of leaves will appear at ground level, like in a lettuce. Such ground-level whorls are called **basal rosettes**. If the whorl of leaves develops on an axillary bud, then it is called a **brachyblast** (from the greek *brachy*, short, and *blastos*, shoot or sprout).

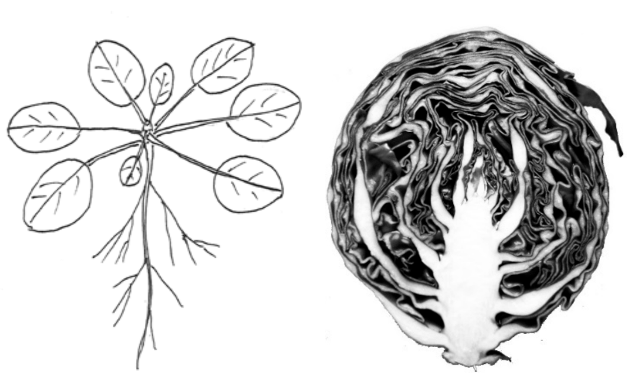


Figure 2.2. Short shoots: Basal rosette growth in *Chorizanthe rigida*, a desert annual (left), and shortened stem and whorl of fleshy leaves forming the "head" of a cabbage.

The stem system

Within this general modular growth achieved by the iterative repetition of metameres (node + internode → node + internode → node + internode → node + internode →...), plants have evolved stems adapted to some very specific functions. Stems may be either aerial (i.e., above-ground) or subterranean (below-ground). **Aerial** stems may be **herbaceous** if they remain soft and produce little secondary growth, or may be **woody** if they produce hard, lignified secondary growth and are covered with bark. In some groups, like cacti, stems are **succulent**, that is, they contain large amounts of soft, water-storing tissues. Climbing plants coil around other plants or inanimate objects as a means of support, and their stems are often transformed into **tendrils**, or twining shoots. Similarly, low-lying plants often have horizontal stems called **stolons** running on the ground and rooting at the nodes from where the foliage leaves sprout. Finally, many dryland trees have stems transformed into spiny **thorns**, or sharp-pointed stems that defend the plant from herbivores. In short, within the general theme of supporting the photosynthetic canopy and connecting the leaves from the roots through the vascular system, the aerial stem system can show some very specialized traits that allow the plant to prosper in very specific environments. The general appearance of the aerial stems determines the **habit** of the plant, also known as the **growth-form** or the **architecture** of the plant.

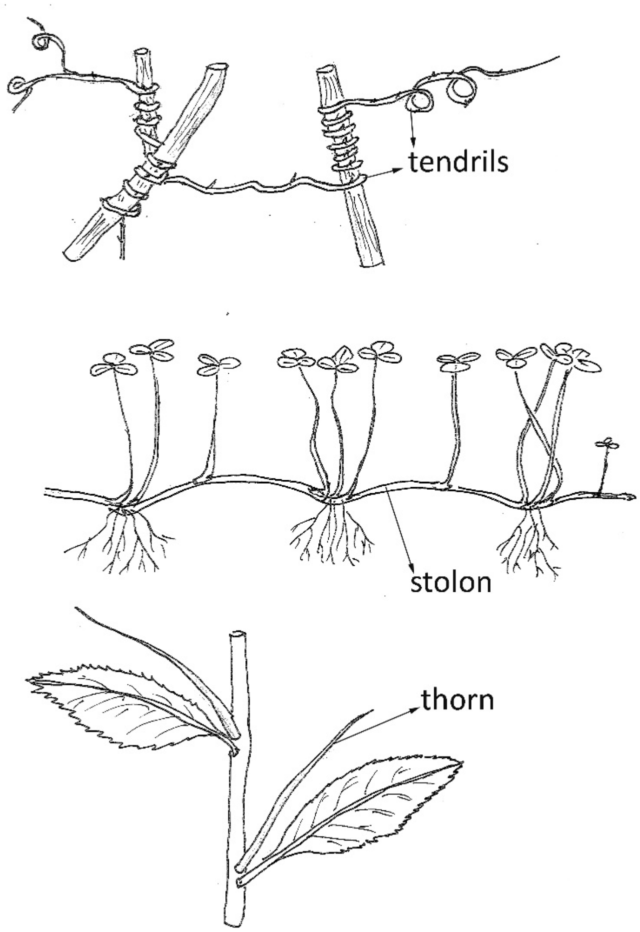


Figure 2.3. Specialized aerial stems: Tendrils, stolons, and thorns.

Subterranean stems, because of their location, are often confused with roots. The presence of nodes, internodes, leaf scars, and axillary buds on these underground structures are key traits to distinguish them from true roots. They have evolved mostly as a result of selective pressures to protect the plant from predatory herbivores, and they fulfil two roles: (a) Long underground stems, called **rhizomes**, vegetatively multiply the individual plant by allowing it to spread out underground, protected from predators, until it eventually emerges to the surface and forms a new individual. (b) Other subterranean stems, like **bulbs** and **tubers**, store nutrients and energy in the form of starch. The stored reserves will allow the plant to rapidly re-sprout at the beginning of the following growth season. **Bulbs** are underground short shoots with fleshy, overlapping leaf bases attached to a small basal stem, as in the onion. **Tubers**, in contrast, have very reduced scaly leaves and a thick, starchy stem axis, as in the potato.

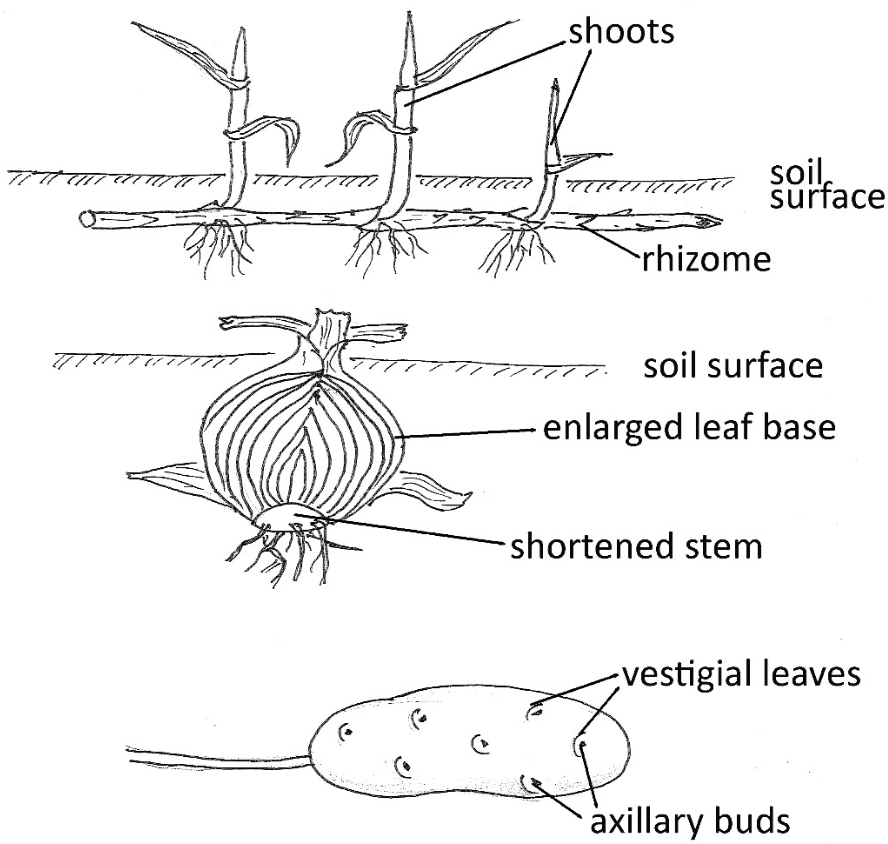


Figure 2.4. Specialized underground stems. Top: rhizome in Johnson-grass, a weedy invasive. Center: onion bulb, highlighting the basal short shoot and the succulent leaf bases. Bottom: potato tuber, showing the axillary buds and the vestigial leaf-scars, which betray its true origin as a stem, not a root.

Growth habits

At this point, it should be apparent that, despite the fact that all seed plants follow essentially the same pattern of modular growth, there are marked disparities between different species. An oak tree, for example, looks radically different from, say, a cabbage. If both species have the same type of modular growth, and the same body plan, how can they be so different? There are three main parameters that are regulated during plant growth that drive these apparently unrelated plant architectures: (a) First, and foremost, internode length can vary from species to species and create vastly contrasting life forms. Rosette plants, such as cabbage or lettuce, have extremely short internodes, giving the appearance of having no stem. (b) Secondly, the profuseness of branching and the angle new branches make with the main stem may also contribute immensely to the overall shape of the plant. (c) Lastly, the arrangement of leaves in space, and the shape and size of the leaves, will give a distinct appearance to the plant's canopy.

For example, the apparently immensely complex shape of a cactus is simply the result of internode shortening and the transformation of leaves into spines (Figure 2.5). Similarly, the difference between open-canopy trees, canopy-dense specimens, droopy-branched individuals, or wind-swept ones is simply related to the internode length and the angle of branching. Trees with the same number of branches may look bizarrely different only by varying these two parameters (Figure 2.6). Like a Lego® puzzle, the plant's basic modules —node, axillary bud, and internode— are extremely simple, but their arrangement in space can look incredibly complex.

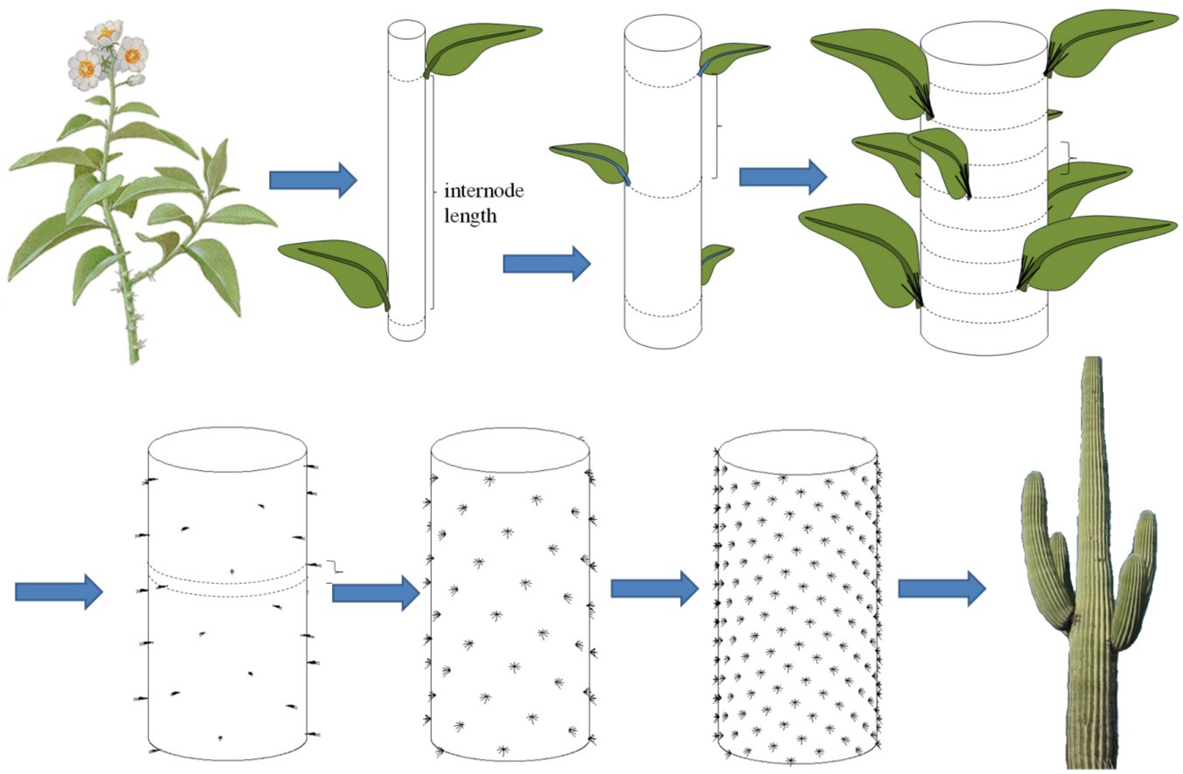


Figure 2.5. Morphological evolution of the cactus stem: Gradual shortening of the internodes and reduction of the leaves into spines makes the transition from an ancestral leafy plant (*Pereskia grandiflora*) into the cactoid stem form of the sahuaro (*Carnegiea gigantea*).

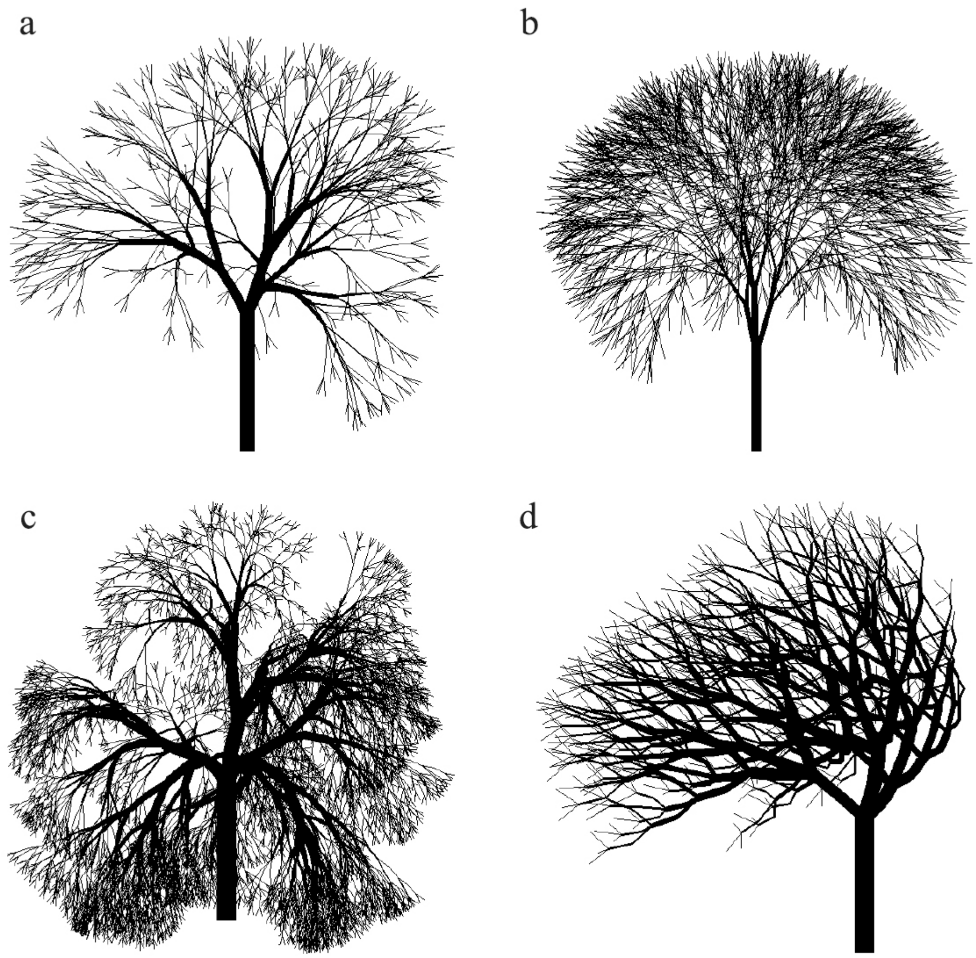


Figure 2.6. Fractal "trees". Simple mathematical models show that plants with the same number of stems and branches, differing only in the length of the internodes and the angle of branching, can acquire radically different life forms (from *The Algorithmic Beauty of Plants*, by P. Prusinkiewicz, 2004).

According to the general morphology of the stem, plants can be classified into five broad categories of growth forms, or **habits**: (1) **Herbs** are plants with green, non-woody stems that die back each year at the end of the growing season. (2) **Shrubs** are low, woody perennials with more than one principal stem arising from the ground. (3) **Trees** are usually large, woody perennials with a single main stem or trunk supporting a leafy canopy above. (4) **Vines** are herbaceous climbers with elongated, flexible, non-self-supporting stems, which, like all herbs, die back at the end of the growing season. (5) **Lianas**, in contrast, are woody climbers with elongated, flexible, non-self-supporting stems that grow using other trees for support.

These basic growth forms are often given adjectives to further describe their growth habits. **Caespitose** plants form ground-level mats, as in the common white clover (from the Latin *caespes*, meaning turf or sod). **Climbing** stems ascend upon other plants or objects by means of flexible, coiling stems. **Spreading** plants have widely open branches, oriented outwards and diverging from the central stem. **Prostrate** plants have branches that lie flat upon the ground. Finally, **twining** stems coil around other plants or non-living structures as a means of support.

Duration of plants and plant parts

Plants are also often classified according to the duration of their growth cycle into four categories: (1) **Ephemeral** plants are extremely short-lived, living only for a few weeks, such as many desert spring flowers that spend most of their time in the form of seed; they germinate and grow after spring rains in a few weeks to rapidly produce new seeds and die. (2) **Annual** plants live for one year or less, and are mostly herbaceous in their growth habit. (3) **Biennial** cycles are often observed in wild lilies, which live for two years, growing vegetatively the first year to store nutrients in their bulbs, and then flowering and fruiting abundantly during the second year. (4) Finally, **perennial** plants are mostly woody trees and shrubs that live for three or more years, and often for very long times.

Plant parts also have a cycle of their own. Leaves, for example, are produced in some plants in spring and are shed in fall, while other plants retain leaves year round. Plants that shed their leaves in winter are called **deciduous**, while plants that remain green during the dormant season are called **evergreen**. Other plant parts, such as fruits or flowers, can be shed or retained according to the particular life history of each species. Plant parts which fall off easily are also called **deciduous**, while parts that remain attached for long periods are called **persistent**. For example, the fruits of the California fan palm are deciduous, while the seed capsules of the Joshua tree are persistent.

The root system

As a result of their underground nature, roots are difficult to study and the root system of flowering plants has a rather meager terminology. The most commonly described trait is the organization of the root system: **Fibrous** roots are seen in plants in which all of the roots are of about the same size so that none is clearly dominant, as in most monocotyledons. **Tap** (also known as **pivot**) root systems, in contrast, have a central root that is clearly larger than the others, as in most dicotyledons. Some plants use their roots to store carbohydrates (mostly starch), nutrients, and water. These storage roots are called **tuberous** roots, as in sweet potatoes or turnips.

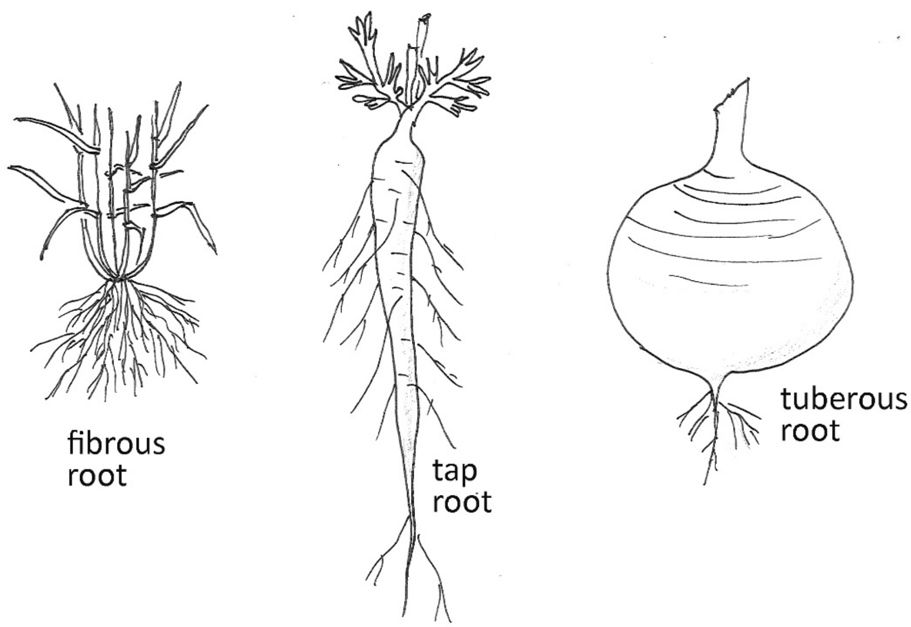


Figure 2.7. Root types: Fibrous roots, tap roots, and tuberous roots.

Adventitious roots (from the Latin *adventicius*, coming from elsewhere) are not produced from the base of the stem, but rather from nodes away from the base, as in ground-level stolons (Figure 2.3). Adventitious roots typically form in the internodes of ground-creeping stolons in plants such as white clover or strawberries. **Aerial** roots are a particular case of adventitious roots occurring above ground, as in the climbing ivy. In some plants that grow entirely out of the soil, such as orchids, aerial roots receive water and nutrients directly from raindrops, fogs, dew, or humidity in the air. Other aerial roots are used mainly for structure, functioning as prop roots, as in maize, or anchor roots, as in the strangler fig.

LEAVES

In most vascular plants, the leaf is a broad flattened photosynthetic organ. Leaves vary greatly from one species to another, so understanding and recognizing leaf features is important in plant identification.

Parts of the leaf

The leaf is essentially formed by two parts: (a) a flattened expanded portion called the **blade**, or **lamina**, whose main function is to capture light, and (b) a stalk, called the **petiole**, that supports the leaf and connects it to the stem. The petiole contains vascular tissues through which the leaf receives water and nutrients from the soil, and exports the products of photosynthesis to the rest of the plant. In many dicotelydon plants, leaves have a pair of appendages called **stipules**, located at point where the petiole joins the stem.

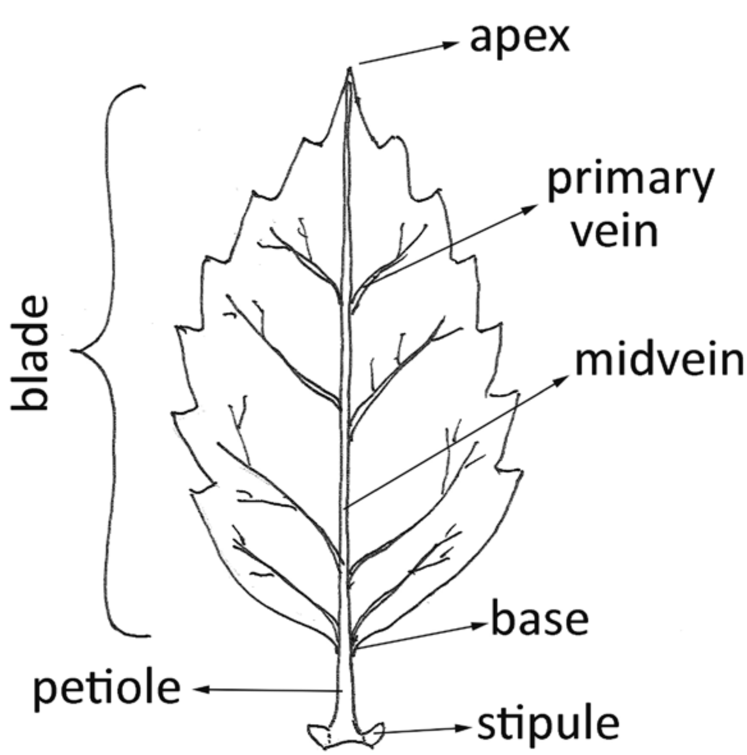


Figure 2.8. Parts of the leaf.

The upper side of the leaf is normally dark-green and shiny. Its surface is specialized in capturing light, so it has distinct optical properties and a smooth, often shiny, surface layer. In contrast, the lower side of the leaf frequently looks rougher and has a lighter color. If we observe it in the microscope, we will see that it is full of small pores called **stomata**, through which the plant captures atmospheric CO_2, necessary for photosynthesis, and releases oxygen as a by-product. The lower part of the leaf is specialized in exchanging gases with the atmosphere, so optical properties are not very important but physical boundary-layer conditions, such as surface rugosity or hairiness that act as windbreakers, are important in order to prevent excessive water loss.

Leaf arrangement

Leaf position with respect to neighboring leaves

Because the main role of leaves is to intercept light as efficiently as possible, plants have evolved very distinct types of spatial arrangement of their leaves, minimizing competitive shading between neighboring leaves in the same plant. The spatial arrangement of leaves with respect to each other is called **phyllotaxy** (from the Greek *phyllos*, leaf, and *taxis*, order). Plants with **alternate** leaves have one single leaf at each node, and successive leaves along the stem are separated by an angle of around 137° (known as the "Fibonacci angle"), forming a spiral arrangement. When two leaves are produced at each node, the leaf disposition is **opposite**. In most plants with opposite phyllotaxy, the leaf pairs at each node alternate at right angles with the leaf pair in the preceding node, forming a **decussate** leaf arrangement (from the Latin *deca*, meaning "ten," because the cross-like pattern of the leaf arrangement when viewed from above resembles the roman number X, or 10). Some plants have **distichous** phyllotaxy, the leaves appear on opposing sides of the stem and in the same plane, giving the whole plant a flat or palm-like appearance. Finally, plants that have whorls of three or more leaves at each node are called **whorled** or **verticillate** (a **verticil** is a whorl or circle of leaves, bracts, or flower parts).

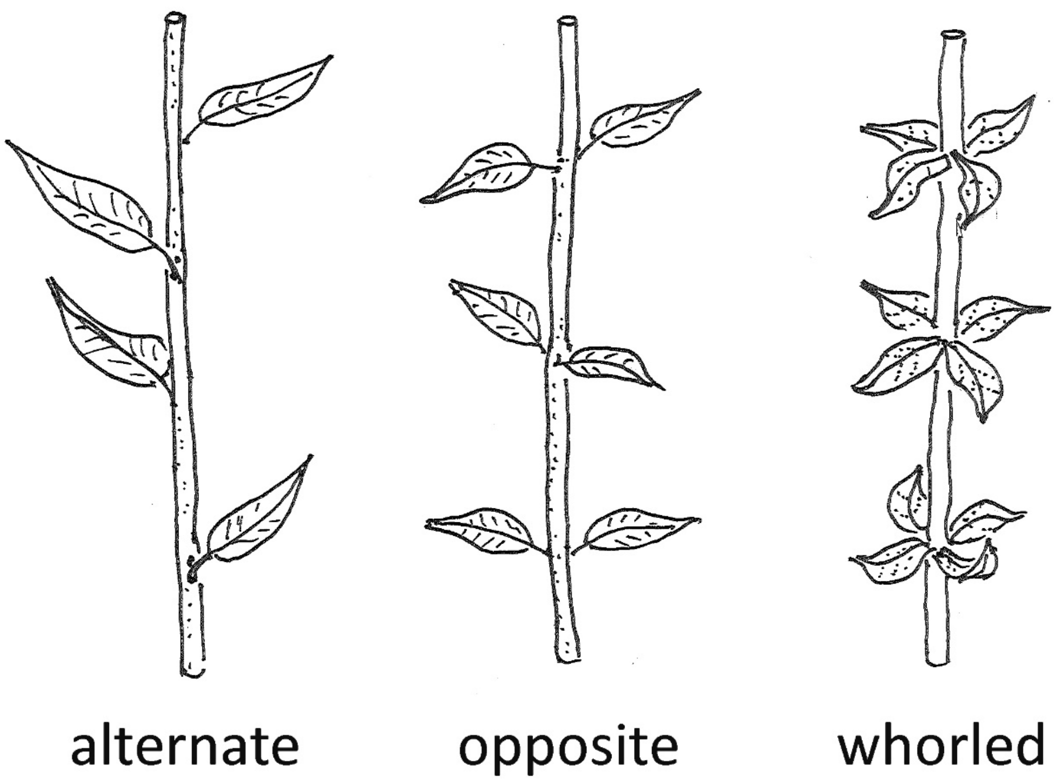


Figure 2.9. Main modes of phyllotaxy, or leaf arrangement.

Leaf position along the stem

Many herbaceous plants have a distinct life cycle, in which the plant grows at first in the form of a basal rosette (that is, a whorl of leaves on a shortened stem near ground level) and later develops a long flowering stem rapidly ascending with long internodes. In these plants, distinguishing the position of the leaves along the stem can be an important trait to identify them in the field. **Basal** leaves occur at the base of the plant, at a stage in which the internodes are reduced and the canopy forms a basal rosette. In contrast, **cauline** leaves (from the Greek *caulon*, stem) occur on a well-developed stem, separated by long internodes.

Figure 2.10. Rosette of basal leaves and smaller cauline leaves in *Duddleya cymosa* (courtesy of the California Dept. of Fish & Wildlife: https://www.wildlife.ca.gov/Conservation/Plants/ Line-Drawings).

Composition: simple vs. compound leaves

Leaf blades can be **simple** or **entire**, when the leaf has a single, undivided blade, or **compound**, when the leaf is divided into two or more discrete segments and appears to have multiple blades. Simple leaves may exhibit various degrees of indentation, often approaching the appearance of compound leaves. A leaf is **lobed** when it is indented about one-fourth to almost half way of the blade; or **parted** when it is divided nearly all the way to the central vein of the blade.

Compound leaves are divided into separate segments called **leaflets** or **folioles**. The central axis, equivalent to the central vein in a simple leaf, is referred to as the **rachis**. **Pinnate** leaves have a blade divided into leaflets arranged along the rachis. In **bipinnate** leaves the blade is divided twice so that the first order leaflets are themselves further divided into second order leaflets. **Palmately** compound leaves have blades divided into leaflets that radiate from the apex of the petiole, no rachis present, as in the common fan palms. A special case is that of leaves with three leaflets, like the common clover or the poison oak, which can be regarded as both pinnate and palmate. To avoid the confusion, they are referred to as **trifoliolate** leaves.

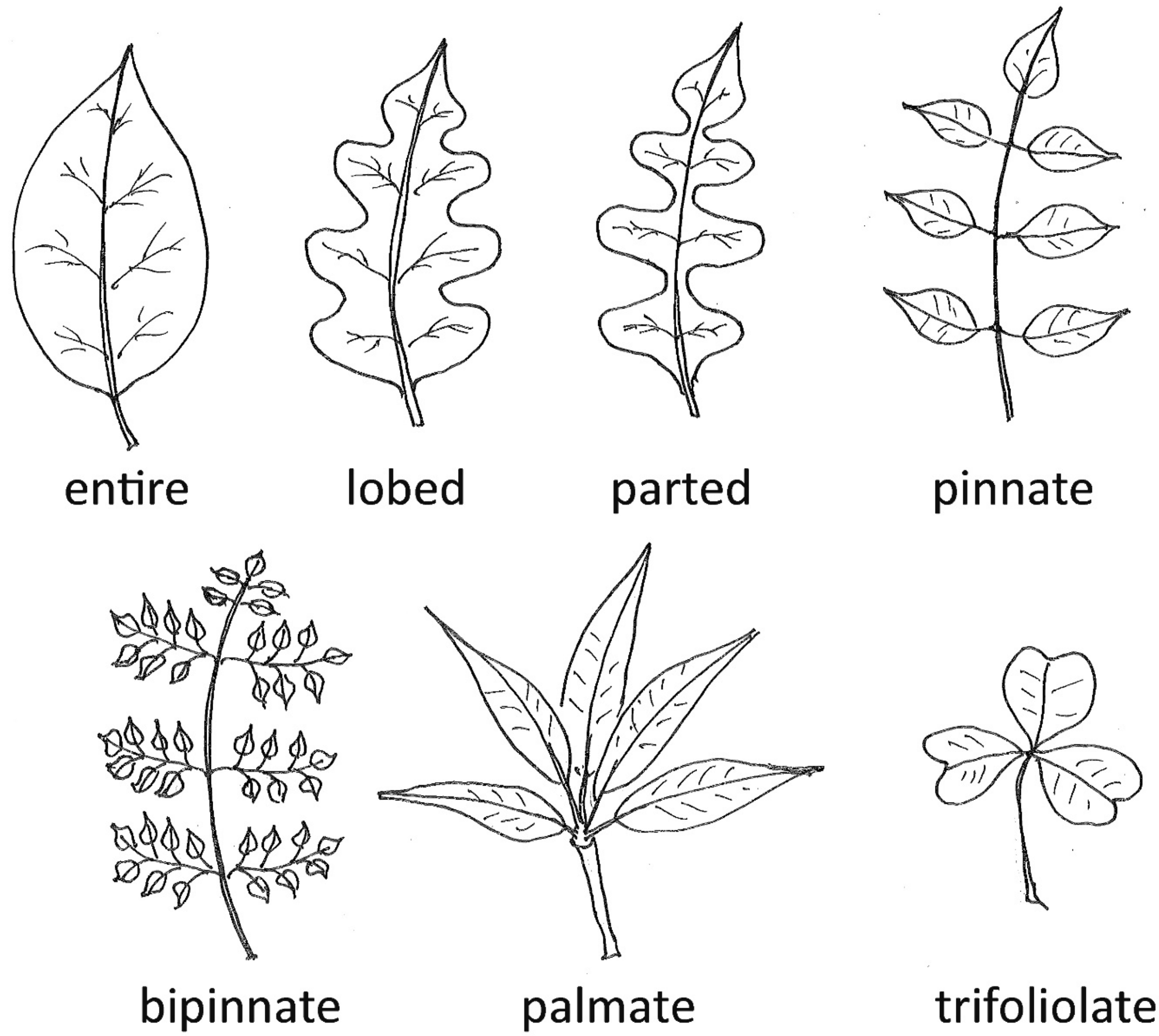


Figure 2.11. Compound leaves.

Leaf shape

Many generalized leaf shapes have been given names, and the list can be long and often tedious to remember. Some names refer to the width-to-length ratio of the leaf, while others refer to the particular design that shapes the leaf perimeter.

Width-to-length proportion: There is a gradient of leaf shapes, from narrow, needle-like leaves to circular shapes. **Acicular** leaves are thin and needle-shaped, as in pine leaves; **linear** leaves (also called **oblong**) are several times longer than wide, with the sides roughly parallel; **oval** leaves are broadly **elliptic**, the length being less than twice the width, and, finally, **orbicular** leaves are circular or nearly so.

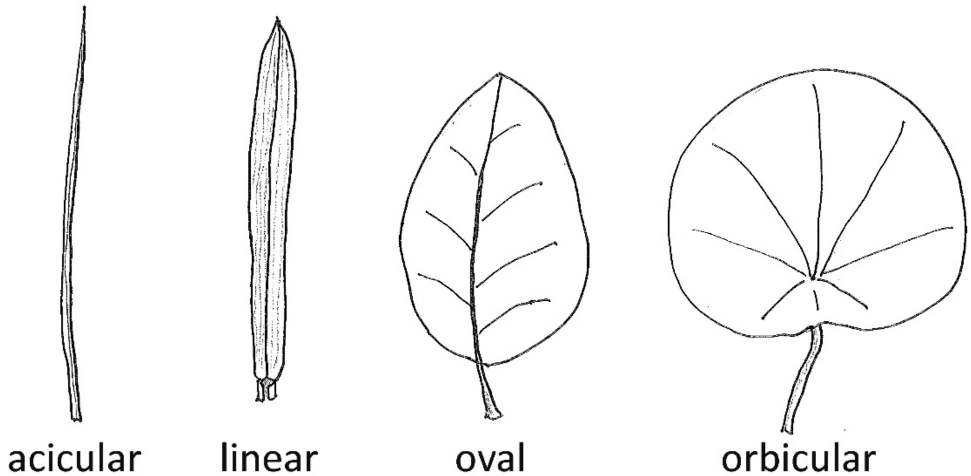


Figure 2.12. Leaf shapes: width-to-length proportion.

Leaf perimeter form: The shape of leaves is described by making reference to common objects. **Cordate** leaves are heart-shaped; **deltoid** leaves are shaped like an equilateral triangle (from the Greek letter delta: ∆); **falcate** leaves are shaped like a sickle (*falcis* in Latin); **lanceolate** leaves are shaped like a lance or spear, several times longer than wide and sides curved with the blade broadest below the middle; **ovate** leaves have the shape of an avian egg, and, finally **sagittate** leaves are shaped like an arrowhead.

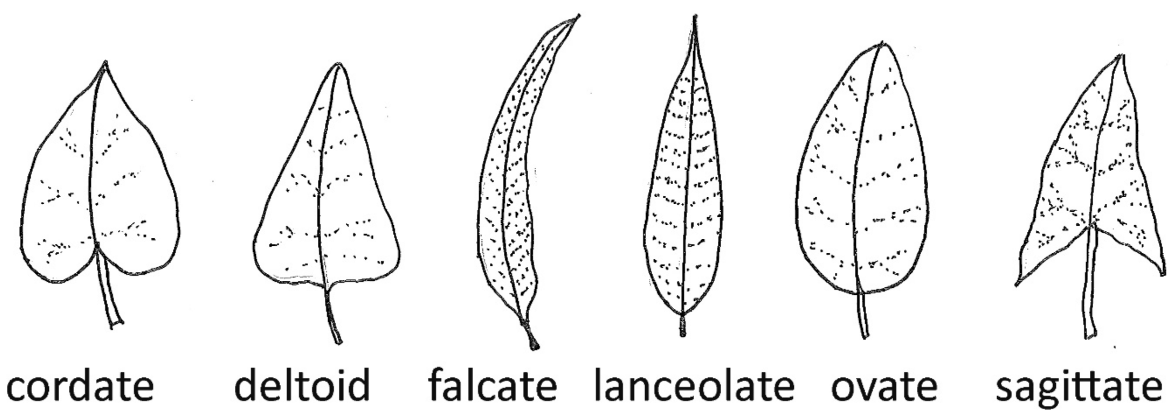


Figure 2.13. Leaf shapes: perimeter form.

Leaf margins

As with the generalized leaf shapes, the list of leaf margin types is long and can become rather complex and convoluted. In a simplified manner, we will recognize the main types: Many leaves have a straight, non-indented edge, called an **entire** margin. In some species, the margin of the leaf is **sinuate**, i.e., making wavy, sinusoidal line. Many other plants have evolved distinct and separate projections called "teeth" along the margin of their blades. If the teeth are rounded and blunt, the leaf is said to **crenate** (from the Latin *crenatus*, notched). If the teeth are coarse and angular, directed outward and perpendicular to the margin, the leaf margin is described as **dentate**. Finally, if the teeth point forward as in a carpenter's saw, the leaf margin is described as **serrate**.

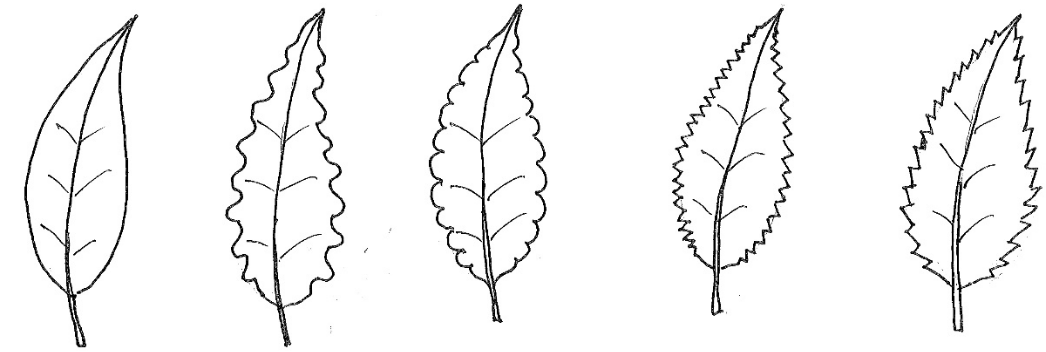


Figure 2.14. Leaf margins.

Venation

The venation pattern shows how the leaf transports water and nutrients into the photosynthetic tissues, and how it exports form them the products of photosynthesis that will feed the rest of the plant. Venation is determined by the arrangement and disposition of the principal veins in the leaf blade. In grasses and lilies (monocotyledons) the most common pattern is a **parallel** disposition, in which several veins of the same size run parallel to one another. In most dicotyledon plants, in contrast, the leaves have a **reticulate** arrangement of veins, in which major and minor veins form a branched, tree-like network, or reticulum. Somewhere in between the geometric simplicity of parallel venation and the network-like complexity of reticulate venation, some plants possess leaves with **pinnate** venation, with a prominent central vein from where a series of lateral veins emerge at an angle along its length. The familiar bird-of-paradise or the banana plants are outstanding examples of this foliar pattern. Finally, in plants where the leaf structures radiate in a fan-like manner from the petiole, as in the maples and the sycamores, the venation pattern is said to be **palmate**.

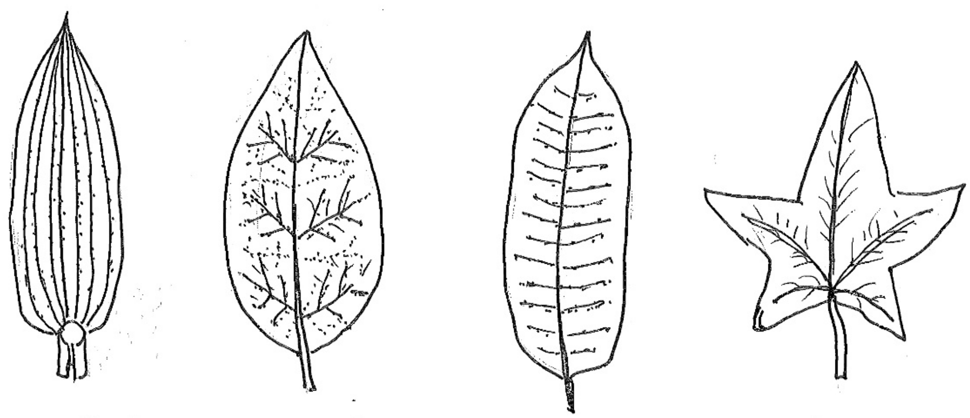


Figure 2.14. Main venation patterns.

The leaf tips: apex and base of the blade

Leaf apices

The upper tip of the leaf, or leaf apex, is an important distinctive character; it is related to the way the leaf drips water, captures dew, or defends itself from predators. The leaf apices can be arranged according to the tapering of the tip, from very sharp to gently rounded. **Spinose** apices, as their name suggests, have a sharp defensive spine at the tip. If the tip is more or less sharp (i.e., the angle is less than 90°), but not spiny, it is said to be **acute**. If the tip is pointed but the angle is more than 90°, then the leaf is said to be **obtuse**. If the apex is gently curved, showing no pointed tip, then the leaf apex is described as **rounded**. Finally, if the tip has a notch (an inwardly-pointed entry rather than an outwardly-pointed tip), then the apex is **emarginated**:

Leaf bases

Like the leaf apex, the leaf base is also an important distinctive character; it is also related to the way the leaf captures water and dew and to how the leaf connects with the stem and the rest of the plant. Several of the same terms used to define leaf apices (such as acute, obtuse, rounded, or emarginated) are also used to define leaf bases. Some additional types of leaf bases, mostly related to the way the leaf embraces the stem, are listed here: **Auriculate** bases have a pair of rounded lobes which somewhat resemble the human ear. **Clasping** bases partly surround the stem, **perfoliate** leaves, such as those of the miner's lettuce in California forests, have no petiole and completely encircle the stem. Finally, some leaves, such as the begonias, are asymmetrical and have one side of the blade larger than the other. Their bases are commonly described as **oblique**, or unequal-sided.

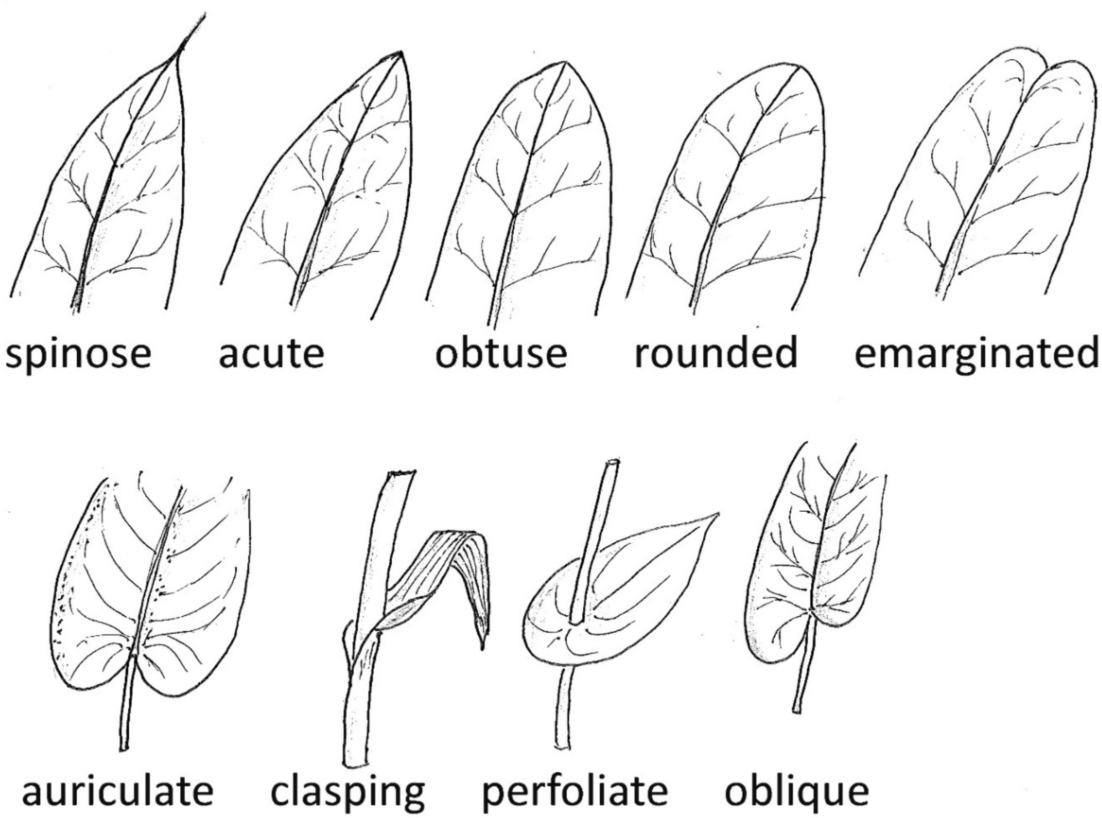


Figure 2.15. Leaf apices and leaf bases.

Leaf modifications

Although the main function of leaves is to intercept light and convert its energy into organic compounds, in many plants leaves have been transformed to perform other, ancillary functions. Many plants show in parts of their stem small, reduced leaves called **bracts**, which play a multiplicity of roles other than capturing light. The following leaf modifications are commonly recognized. Many desert species possess **spines**, which are highly reduced, hard, woody bracts with a sharp point, whose role is to defend the plant against the attack of herbivores and also to reduce water loss through transpiration, a critically important trait in the desert environment. Spines should not be not to be confused with **thorns**, which are modified stems, or with **prickles**, which are mere outgrowths of the epidermis, as in the cultivated rose. Also as part of a the arid-land adaptations to reduce water loss, some woody legumes in the genus *Acacia* (common in the Australian drylands) have lost entirely the blade of the leaf, and retain a flattened leaf petiole, called a **phyllode**, as the basic structure of photosynthesis. Although not as efficient as the leaves in capturing light, the hard and leather-like phyllodes transpire much less and save water in the harsh outback.

In some vines and climbers the leaves have lost parts of the blade, and the petiole and central vein have become an elongated, twining extension of the leaf, capable of coiling around other plants and helping the plant grow above ground with very little metabolic investment in making a solid stem. These highly transformed, coiling leaves are called **tendrils**. In some plants, tendrils may also be of stem, rather than foliar, origin. Finally, in some herbaceous plants, mostly in the grasses and related families, the base of the petiole has become expanded to form a tubular structure that surrounds the stem. These structures, called **sheaths**, provide additional support to the soft, herbaceous stem of these species and allow the meristems, or growing tissues, to stay protected from herbivores near ground level.

Figure 2.16. (left) Evolution of phyllodes (leafy petioles) in *Acacia melanoxylon* from Australia. (right) Foliar tendrils in the tip of the common vetch (*Vicia faba*)

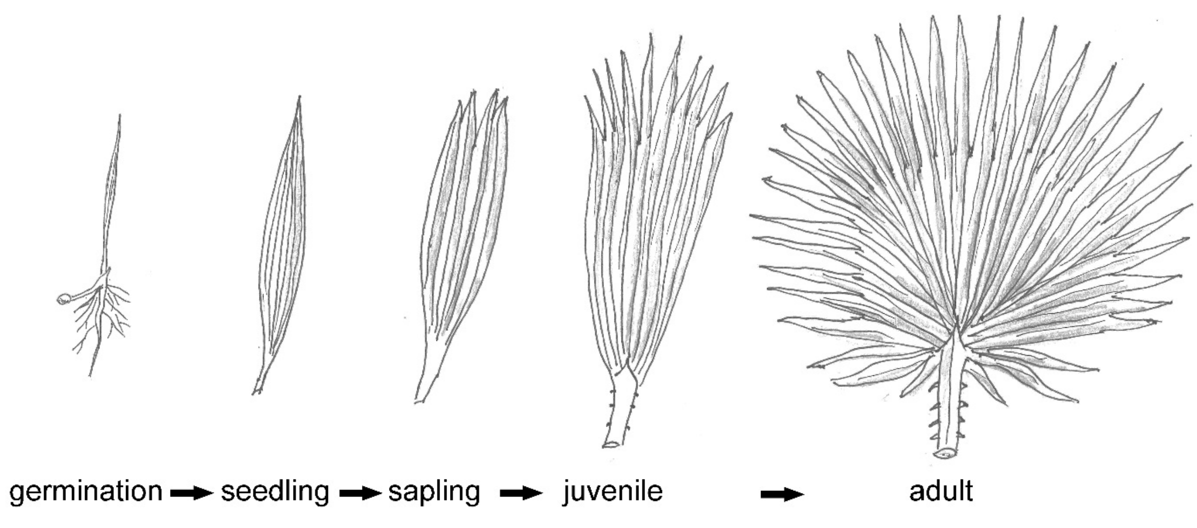
The evolution of leaf form: Ontogeny and phylogeny in fan palms

It is a well-known fact in developmental biology of animals that, in their embryonic stages, widely different species may look very similar, and that this embryonic similarity continues longer in taxonomically related species. It is also known that animal embryos may show traits which they do not have as adults, but which their ancestors possessed. Mammalian embryos, for example, have gill-like pharyngeal folds like those of fish, but they never develop into true gills. Whale embryos, likewise, have primordial hind legs, or "hind limb buds," which are later reabsorbed into the body. These facts were noted by the German zoologist Ernst Haeckel, who famously stated that "ontogeny (the life-history of the individual) recapitulates phylogeny (the life history of the species)." Haeckel believed that the mammalian embryos, for example, were similar to fish embryos in their early stages and then later acquired the traits of reptilian embryos before acquiring true mammalian form. As stated by Haeckel, the Law of Recapitulation has been tested and rejected by modern science. Embryos do not go through all the evolutionary stages before acquiring their own characteristics. Haeckel's "law" is now mostly a curiosity of the history of 19th Century science.

There was, however, some insight in Haeckel's observations. It remains true that it is more likely to observe ancestral evolutionary traits in the early stages of the life cycle of a species than in the adult stages (like the whales' hind legs). This is simply the result of the obvious fact that, because of parental protection, natural selection does not act as intensely in shaping the traits of embryos as it does on adults.

In plants, this means that in many species it is possible to observe ancestral, or "primitive," vegetative characters shortly after the plant germinates, while the adult may show evolutionary novel, or "derived," traits. One striking case where the species' phylogenetic evolution of leaf shape can be observed along the ontogeny, or individual life history, is in the California fan palms of the genus *Washingtonia*. Palms (in the family Arecaceae) belong to the large taxonomic group of the Monocotyledons, together with the grasses and the lilies. Monocotyledons are mostly herbaceous plants, with linear leaves showing parallel venation. How can palms, with their clearly non-herbaceous, massive trunks, and their complex leaves belong in the same group?

In the very early stages of their life cycle, however, palms look very much like a grass, so much so that they are often difficult to identify as palm seedlings: They have no stem, they are herbaceous, and the leaves arise from a ground-level rosette. Furthermore, the leaves are simple, narrow and linear, looking very much like a grass blade. As the plant develops, the new leaf blades become wider, the petiole becomes stouter, the whole leaf takes a lanceolate shape, and the parallel veins become more pronounced. In the next stage, the plant's stalk starts to elongate, producing a fibrous, non-woody stem composed of myriad bundles of conductive tissue, and the leaf blades start cleaving from the tip into multiple folioles, along their longitudinal veins. Finally, in the adult palm the leaves become palmate, with soft-green folioles inserted on a stout petiole that supports the whole, and now quite complex, leaf. The evolution of the taxon, from an ancestral grass-like plant to tall palm with massive trunks and fan-like leaves can be understood simply by looking at the life-history of individual plants.



Leaf surfaces and surface coverings

Leaf and stem surfaces

The surface of stems, leaves, flowers, fruits and seeds reveals many useful features. The following terms are applied: The term **glabrous** is generally used for leaves without hairs. **Dull** leaves are non-shining, or lacking lustre, while **lustrous** leaves have a smooth, shining epidermis. Many plants defend their leaves from excessive transpiration with a coat of wax, which usually gives them a dull whitish bloom, called a **glaucous** surface. Other plants prevent excessive transpiration with a resin coat on their epidermis, which gives the leaf a **viscid**, or sticky appearance. Although the surface of most leaves is smooth, in some plants the leaves have an uneven surface: **rugose** leaves are wrinkled, **striated** leaves are marked with longitudinal grooves, and **tuberculate**, or **verrucose**, leaves show wart-like lumps.

Leaf surface coverings: plant hairs

Leaf surfaces, no matter what their type, may be clothed with hairs of some sort. Plant hairs are technically referred to as **trichomes.** The types of trichome coverings are numerous and their classification is very complex, perhaps more subjectively defined than the other vegetative features described in this chapter. Only a few simple types of plant hairs will be described here: Some plant show hooked hairs in the epidermis of their leaves or fruits, which attach to the fur of many animals like Velcro® fabric. These hooked structures are made up of **uncinate** trichomes that serve chiefly for the dispersal of plant parts. There is a continuum in the stiffness of plant trichomes: **lanate** (also known as **tomentose**) leaves are covered by a soft mat of woolly-cottony trichomes; **pubescent** leaves are also soft and downy, but their hairs are short and erect, as in velvet fabric; **scabrous** (or **hirsute**) leaves are rough to the touch because of coarse, stiff, ascending hairs, as in an unshaven male face. Finally, **glandular** trichomes are hairs with swollen, gland-bearing tips that often are strongly sticky to the touch, as in many carnivorous plants that use glandular hairs to attract insects.

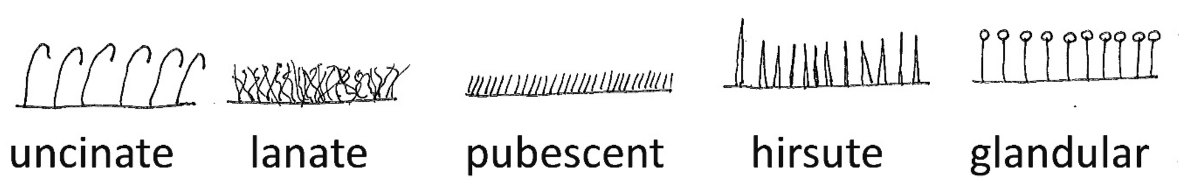


Figure 2.17. Main types of plant hairs.

GLOSSARY

MODULAR GROWTH

nodes: the point of attachment of leaves and buds onto the stem

internodes: stem segments between two successive nodes

leaves: flattened photosynthetic organs consisting of blade and petiole

blade (=**lamina**): flattened expanded portion of the leaf

petiole: stalk supporting the blade and attaching the leaf to the node

sessile: seating, lacking a petiole

stipules: pair of appendages at base of petiole

axil (from the Latin *axilla*, underarm pit): angle of insertion between the leaf and the stem

axillary bud: an immature group of undifferenciated cells (stem cells), or meristem, forming a bud from where new growth and new branching may occur

LONG SHOOTS, SHORT SHOOTS

basal short shoots (=**rosettes)**: whorl of leaves tightly packed around a central axis

axillary short shoots (=**brachyblast**; from the greek *brachy*, short, and *blastos*, sprout): whorl of leaves, or rosette, that develops from an axillary bud

STEM FUNCTION

Aerial stems

stolon (=**runner**): a horizontal stem, often rooting at the nodes, bearing leaves

tendril: a twining stem, either terminal or arising from an axillary bud

thorn: a sharp-pointed stem

Subterranean stems

bulb: an upright series of fleshy overlapping leaf bases attached to a small basal stem, as in the onion

rhizome: a horizontal stem with reduced scaly leaves, as in many grasses

tuber: an enlarged fleshy tip of an underground stem, as in the potato

ROOT FUNCTION

fibrous: a root system in which all of the roots are of about the same size so that none is clearly dominant, as in many monocots

tap: a root system in which one root is clearly larger than the others, as in many dicots

tuberous: a root that is particularly large and fleshy, and underground storage root

adventitious (from the Latin *adventicius*, foreign): roots arising from any point along the stem

aerial: roots occurring above ground

HABIT

General growth habits

herbs: plants with non-woody aerial stems which die back to the ground each year

shrubs: woody perennials with more than one principal stem arising from the ground

trees: woody perennials with a single main stem or trunk

vine: herbaceous plants with elongate, flexible, non-self-supporting stems

lianas: woody plants with elongate, flexible, non-self-supporting stems

Types of stems

caespitose: turf-forming, growing in tufts or mats

climbing: ascending upon other plants or objects by means of special structures, such as tendrils

spreading: oriented outward and more or less diverging from the point of origin

prostrate: lying flat upon the ground

twining: coiling around plants or objects as a means of support

DURATION

Life cycle

ephemeral: short-lived, living only for a few weeks

annual: living for one year or less

biennial: living for two years, typically flowering and fruiting the second year

perennial: living for three years or more

Shedding of plant parts

deciduous: plants which shed all their leaves at the end of each growing season; also applied to plant parts which fall off

evergreen: remaining green during the dormant season, the plants never without some leaves

persistent: remaining attached and unwithered

PARTS OF THE LEAF

blade (=**lamina**): the flattened expanded portion of the leaf

petiole: the stalk which supports the lamina; if missing, the leaf is **sessile**

stipules: a pair of appendages often located at the base of the petiole where it joins the stem

LEAF ARRANGEMENT (=PHYLLOTAXY)

Leaf position with respect to neighboring leaves

alternate: one leaf at each node

opposite: two leaves at each node

decussate: opposite leaves which alternate at right angles to one another at successive nodes

distichous: two-ranked on opposing sides of the stem and in the same plane

whorled (=**verticillate**): in whorls (also called verticils) of three or more leaves at each node

Leaf position along the stem

basal: leaves at the base of the plant, the internodes being much reduced forming a basal rosette

cauline: leaves on a well-developed stem, separated by long internodes, as opposed to basal leaves

LEAF COMPOSITION: SIMPLE VS. COMPOUND LEAVES

simple: leaf has a single, undivided blade

lobed: leaf blade is partially indented up to half way of the blade

parted: leaf blade is nearly all the way to the central vein

compound: the leaf is divided into two or more discrete segments and appears to have multiple blades

leaflet (or **foliole**): each of the segments of a compound leaf

rachis: the central axis of a compound leaf, equivalent to the central vein in a simple leaf

pinnate: leaves divided into leaflets arranged along the main rachis

bipinnate: leaves divided into first order leaflets, which are themselves further divided into second order leaflets

palmately-compound: leaves divided into leaflets that radiate from the apex of the petiole, no rachis present, as in the common fan palms

trifoliolate: a compound leaf with three leaflets, as in the common clover

LEAF SHAPE

Width-to-length proportion

acicular: needle-shaped, as in pine needles

linear (=**oblong**): several times longer than wide, the sides more or less parallel

oval: broadly elliptic, the length less than twice the width

orbicular: circular or nearly so

Leaf perimeter form

cordate: heart-shaped, with the petiole attached between the basal lobes

deltoid: shaped like an equilateral triangle (the greek letter delta Δ)

falcate: sickle-shaped

lanceolate: lance-shaped, several times longer than wide; the sides curved, with the blade broadest below the middle

ovate: the shape of a chicken's egg, with the petiole at the broad end

sagittate: arrowhead-shaped

LEAF MARGINS

entire: not in any way indented, the margin featureless

crenate: scalloped, the teeth blunt

dentate: with coarse angular teeth directed outward at right angles to the margin

serrate: with coarse saw-like teeth which point forward

sinuate: wavy in and out, in the plane of the blade

VENATION

parallel: several veins of the same size and parallel to one another, as in grasses and lilies

pinnate: prominent central vein with a series of major veins arising at an angle along its length

reticulate: major and minor veins forming a branched network or reticulum

palmate: major veins radiating from a common point at the base, as in the maples

LEAF TIPS: APEX AND BASE

Leaf apices

- **spinose**: with a spine at the tip
- **acute**: apex formed by two straight margins meeting at less than 90°
- **obtuse**: apex formed by two lines which meet at more than a right angle
- **rounded**: the apex gently curved
- **emarginated**: with a shallow notch at the apex

Leaf bases

- **auriculate**: with a pair of rounded lobes which somewhat resemble the human ear
- **clasping**: the bases partly to completely surrounding the stem
- **perfoliate**: the condition of a sessile leaf when the base completely encircles the stem
- **cuneate**: wedge-shaped
- **oblique**: asymmetrical; unequal-sided

LEAF MODIFICATIONS

bract: a leaf much reduced in size, particularly if it is associated with a flower or inflorescence

spine: a leaf or portion of a leaf which is sharp-pointed

tendril: a twining leaf or portion of a leaf, as in the leaflets of the sweet pea; tendrils may also be of stem origin

phyllode: a leaflike petiole of a bladeless leaf, as in some *Acacia* trees from the Australian drylands

sheath: the basal portion of the leaf which surrounds the stem, as in the grasses

SURFACES AND SURFACE COVERINGS

Leaf and stem surfaces

- **dull**: not shining, lacking lustre

glabrous: without hairs

glaucous: covered with a whitish waxy bloom

lustrous: shining

rugose: wrinkled

striated: marked with longitudinal lines

tuberculate (=**verrucose**): warty

viscid: sticky

Leaf surface coverings: plant hairs

uncinate: hooked hairs, as in Velcro® fabric.

lanate (=**tomentose**): woolly or cottony, densely and softly matted

pubescent: downy; the hairs short, soft, and erect

scabrous (=**hirsute**): rough to the touch because of coarse, stiff, ascending hairs

glandular: hairs with swollen tips; gland-bearing