Microworld of leaves: pdf document

This compressed pdf document provides a users-friendly print-outline of the English version of the "Microworld of Leaves", a virtual tour related to questions on the anatomy of leaves. The tour contains more than 100 thumbnail pictures. In the original html version these pictures can be clicked to produce larger images with additional labels or to activate animations. The virtual tour is part of the Virtual Classroom of Biology (University of Nijmegen) (http://www-vcbio.sci.kun.nl).

Contents

1. Generalities

1.1. Introduction

Biology is a highly versatile part of science. The teaching and research in Biology at the University of Nijmegen cover a large diversity in topics and often utilize sophisticated techniques. However, a lot of exciting observations on the living world may still be gained with simple means at school or at home. Accordingly, many of the data presented in this virtual tour through the microworld of the leaf can be obtained with a simple student light microscope.

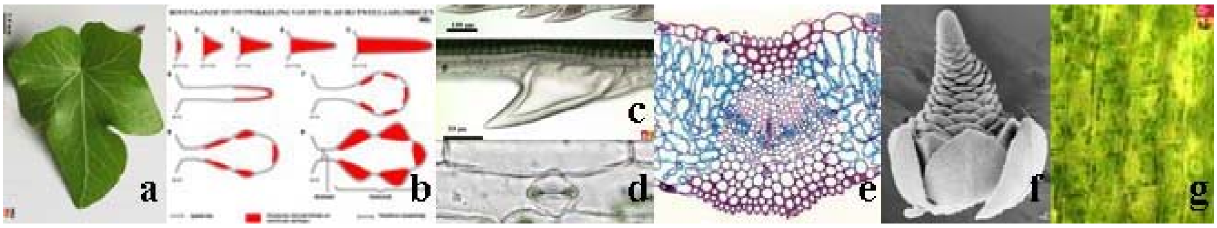

Figure 1. A few examples of figures shown in the virtual tour "The microworld of leaves". a. Close-up view; b. Illustration; c and d. Light microscopy of fresh material; e. Light microscopy of stained section; f. Scanning electron microscopy; g. Movie

Leaves are known to all of us, but did you realize that nearly all life forms on earth ultimately depend on the activity of plant leaves and algae? Leaves catch light energy and convert it into chemical energy to produce organic compounds, a process called photosynthesis. How are leaves able to in produce biomaterial? How are they able to perform so well even under the most extreme climates and weather conditions? Leaves may occur in all kind of sizes and shapes, but can still be identified as leaves. Despite the diversity in morphology what do all leaves have then basically in common? How are leaves formed? These are some of the questions that are addressed in this richly illustrated tour (Fig. 1) focused on the micro-anatomy of leaves.

1.2. Sources

Esau K. 1963. Plant anatomy. John Wiley and Sons. New York, London. 735 pp.
Raven P.H., Evert R.F. and Eichhorn S.E. 1999. Biology of plants. W.H. Freeman and Company. New York. 944 pp.

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1.4. Copyright and disclaimer

2. Leaf architecture

2.1 Photosynthesis and anatomy

Plants occupy a fundamental position in the food web, since they serve as the primary source (producents) of organic compounds for animals and humans. Plants utilize their leaves to produce sugars in a process that involves light and which is called photosynthesis. Simplified (Fig. 2), water (H_2O, the source of H and O) and carbon dioxide (CO_2, the source of C) are transformed into sucrose (a sugar; $C_6H_{12}O_6$) and oxygen (O_2; to the atmosphere) in a process in which light energy is consumed.

$6CO_2$	+	$6H_2O$	$\xrightarrow{\text{light}}$	$C_6H_{12}O_6$	+	$6\ O_2$
Carbon dioxide	+	Water	$\xrightarrow{\text{light}}$	Sugar	+	Oxygen

Figure 2. Simplified net photosynthetic reaction

Photosynthesis occurs in the chloroplasts (Fig. 3 d) of the chlorenchyma (or mesophyll tissue) of the leaf (Fig. 5). The whole process requires a logistic performance from the plant (Fig. 5). Water reaches the leaf after translocation from the root through the stem xylem vessels. CO_2 attains the chloroplasts by diffusion from the air through the stomata (pores of the leaf) and the intercellular cavity between the sponge parenchyma cells. The products of photosynthesis, the sugars, are distributed over the entire plant through the phloem vessels. Oxygen liberated from the photo-reaction as well as water molecules leave the plant through the intercellular cavity and the stomata.

In more details, photosynthesis starts with a so-called light reaction. Light energy from the sun is captured by pigment molecules (chlorophyll a, chlorophyll b en carotenes; Fig 3a and b) that are located in the internal membranes (thylakoids) of chloroplasts (Fig. 3c). This energy is consumed to produce reducing power (H^+ ions = protons) and molecular oxygen (O_2) from water molecules (H_2O). The reducing power (the protons) is used to generate ATP (adenosine triphosphate) and NADPH (reduced nicotine amide adenine dinucleotide phosphate). Then, in the so-called dark reaction (a process that does not require light) ATP and NADPH are invested to include CO_2 into organic molecules. The CO_2 fixation and net production of carbohydrates (sugar-like) molecules occurs in the stroma (the fluid part of the chloroplasts) in a complex cascade of reactions named the Calvin cycle (Fig. 3c). Most angiosperms and gymnosperms are so-called C_3 plants, because the first product of CO_2 incorporation is a three-carbon-compound: 3-phosphoglycerate. In C_4 plants, like corn and sugarcane, the Calvin cycle is preceded by fixation of CO_2 into a four-carbon-molecule (oxaloacetate) under control of an enzyme (phosphoenolpyruvate [=PEP] carboxylase) with a high affinity for CO_2. The efficient C_4 mechanism is correlated to a unique leaf anatomy (Kranz anatomy; Kranz = wreath), in which veins are surrounded by a CO_2 fixing bundle sheath, which in turn stays in direct contact with the mesophyll cells where the Calvin cycle occurs.

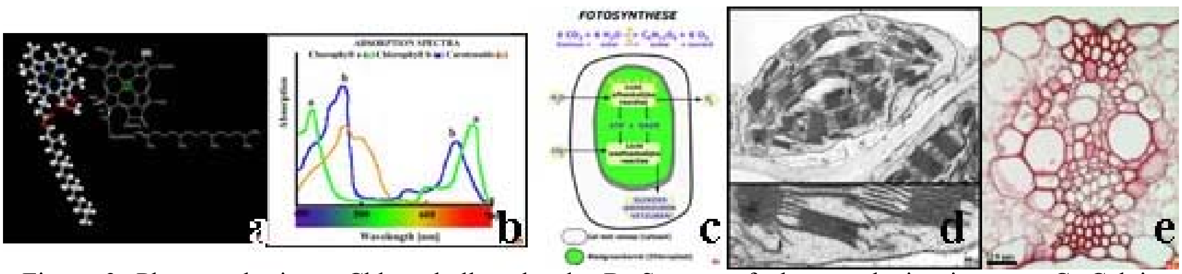


Figure 3. Photosynthesis. a. Chlorophyll molecule. B. Spectra of photosynthetic pigments. C. Calvin cycle. D. Chloroplast. E. Kranz anatomy in corn.

Why do leaves look green in the summer and gold-yellow during fall?

Answer: There is much chlorophyll and carotene in the leaves in summer. These molecules absorb blue and red light and reflect green-yellow light. What you see is this greenish reflected light. In fall, the temperature drops and the production of the red anthocyane in the cell vacuoles raises. Besides, chlorophyll gradually decays, while the more stable yellow, orange and reddish carotene pigments persist and dominate the palette.

2.2. Basic anatomy of the leaf

Leaves have evolved from stem to become a flattened organ with a large and flat blade adequate to capture rays of sunlight for photosynthesis. Full-grown leaves share a basic anatomy, depicted below for ivy, *Hedera helix*. Most leaves show a remarkable so-called bifacial structure, implying that the adaxial side differs from the abaxial side (see further explanations below under veins). In a transverse section of a leaf, several layers can be discerned (Fig. 4):

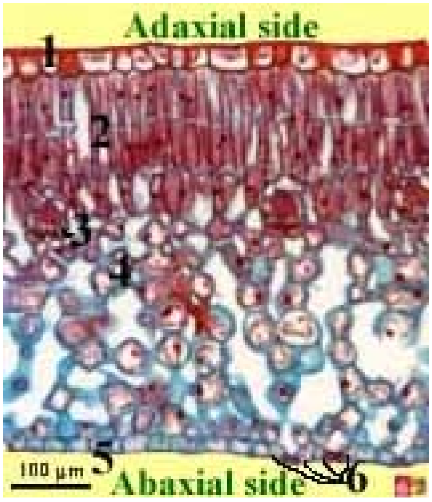


Figure 4. (left- interactive animation in html version)

1 Upper epidermis with cuticle
2 Palissade parenchyma
3.Small vein (vascular bundle)
4 Spongy parenchyma interspaced with cavities
5 Lower epidermis with cuticle
6 Guard cells of the stomata

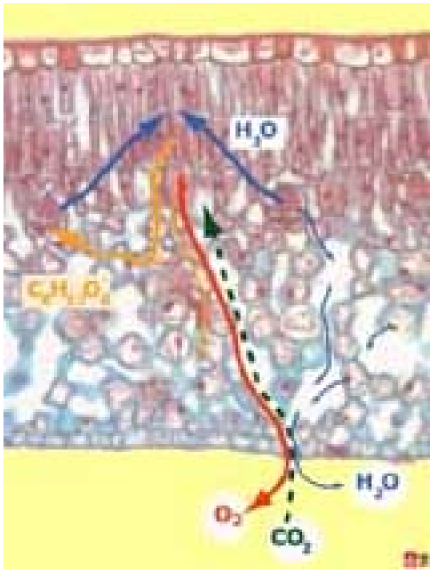


Figure 5. (right)
Flow of substances involved in photosynthesis

2.3. Cell types in leaves

2.3.1.Epidermis (including stomata)

The epidermis is the outermost upper and lower cell tissue. It consists of one or more cell layers. The upper epidermis often differs from the lower epidermis, which related to the exposure to sunlight. Epidermal cells are mostly thick walled, do not contain chloroplasts and form a continuous cover. The epidermis serves to protect the inner tissues against dehydration, intense sunlight (especially ultraviolet light) and mechanical stress. The epidermis also contributes to limit prey by herbivores (insects, cattle) and damage by parasites. The most curious protection mechanisms are provided (Fig. 6), ranging from a multiple cell layer (a), to uni and multi-cellular hairs in all kinds of shapes (c, d, and e), cells with tannins (f), sticky (g), irritating, indigestible or even poisonous substances. Since dehydration is the major threat for plants, the epidermal cells are covered with

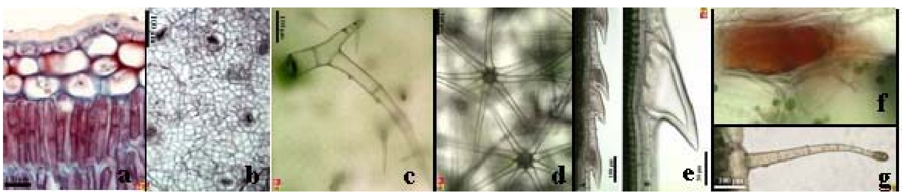


Figure 6. Epidermal cells in leaves. a. Multilayered with thick cuticula. b. Upper view of stomata and epidermis cells covered with a wax plate. c. Multicellular trichome. d. Teeth-shaped trichome. f. Epidermis cell filled with tannin. g. glandular hair.

a cuticle, a layer of cutin, a tough lipid-like and water-impermeable substance (a). In addition, a waxy layer is often present (b).

A special adaptation to land-life is the occurrence in the epidermis of paired guard cells (Fig. 7 a to f) that modulate the opening and closing of the stomata (a kind of port). When guard cells accumulate water they become turgescent like an inflated bean-shaped balloon. Their shape slightly changes so that the stoma opens (Fig. 8. b open; c closed). Water uptake in guard cells in turn is affected by light conditions, air humidity, temperature and the CO_2 concentration. Thus, guard cells control the gas exchange between the interior of the leaf and the environment. In some cases, guard cells are supported by subsidiary cells. In contrast to other epidermis cells, guard cells do possess chloroplasts. Continuously submerged plants lack guard cells and stomata, but achieve gas exchange directly through the normal epidermal cells that bear a thin cuticle.

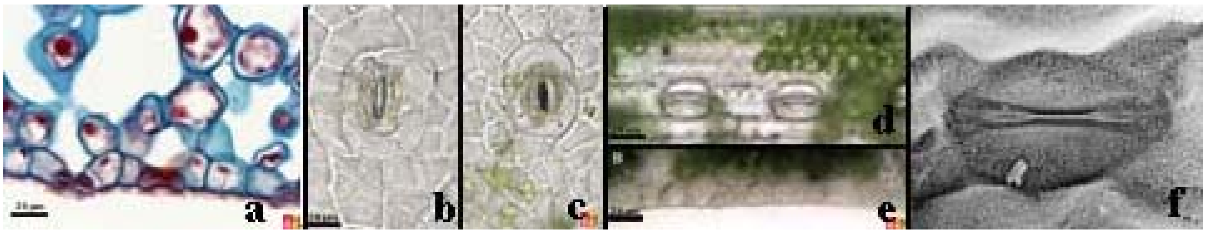


Figure 7. a-f. Guard cells and stomata. a. Cross section. b. closed stoma c Open stoma in a dicot. d. Upper view of an epidermis trip in a monocot. e. Cross section in a monocot. f. Scanning electron micrograph

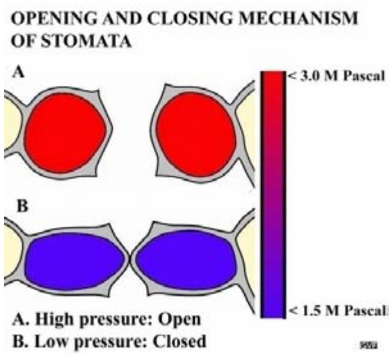


Figure 8. (right. Animation in html version). When guard cells take up water, their pressure increases from 1.5 (blue in B) to 3 mega Pascal (red in A). Since the walls of the guard cells are relatively flexible at the side of the stoma (S), the guard cells expand vertically and the stoma opens (situation in A). Stomata close by a reverse mechanism.

3.3.2. Mesophyll (palisade and spongy parenchyma)

The tissue specialized in photosynthesis is the mesophyll or chlorenchyma (chloroplast-rich tissue; see chloroplast in Fig. 9 c). The mesophyll commonly is differentiated in a palisade and a spongy parenchyma (Fig. 9 a and b).

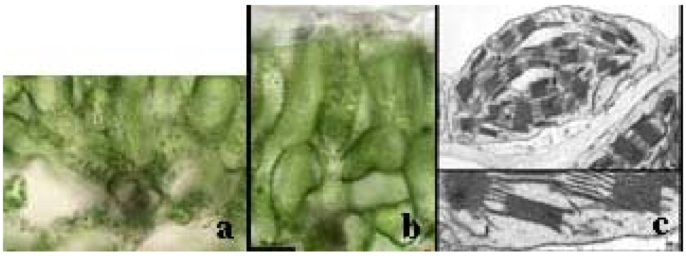


Figure. 9. Mesophyll. a. Spongy parenchyma with intercellular cavities. b. Rod-shaped palisade parenchyma. c Transmission electron microscopy of a chloroplast.

The palisade parenchyma is located directly under the upper epidermis. The cylindrical and elongated cells (or palisades) are at right angles to the epidermis. The spongy parenchyma has an open and net-like structure with large inter-cellular spaces that facilitate gas diffusion. The spongy parenchyma also directly contributes to photosynthesis. The major function of the spongy parenchyma is the transport of oxygen, carbon-dioxide and water vapour. It also is involved in the transport of water and the products of photosynthesis, the sugars. The spongy parenchyma connects the veins with the palisade parenchyma.

2.3.3. Veins - Vascular bundles (xylem and phloem)

The veins or vascular bundles of the leaf are irregularly distributed throughout the mesophyll. The vascular bundles contain xylem and phloem cells (Fig. 10). The xylem transports water from the root through the stem into the leaf. The phloem transports the sugars produced by the photosynthetic reactions to the other parts of the plant.

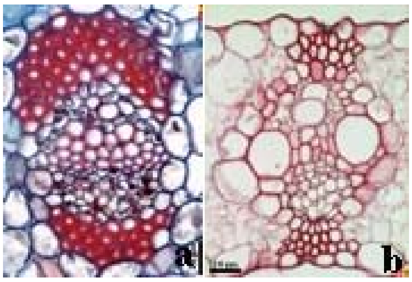


Figure 10. Vascular bundles, in a C_3 plant (a) and in a C_4 plant.

Leaves mostly have a large midrib vein that originates from the stem (Fig. 12). In higher ferns and dicotyl plants the midrib vein branches successively into smaller veins (Fig. 11 a and b for ivy; c and d for petunia) that separate a mosaic of chlorenchyma (chloroplast-bearing cells). Leaves from monocots like papyrus and maize generally have parallel veins (Fig. 11 e and f for papyrus) interconnected by very small veins.

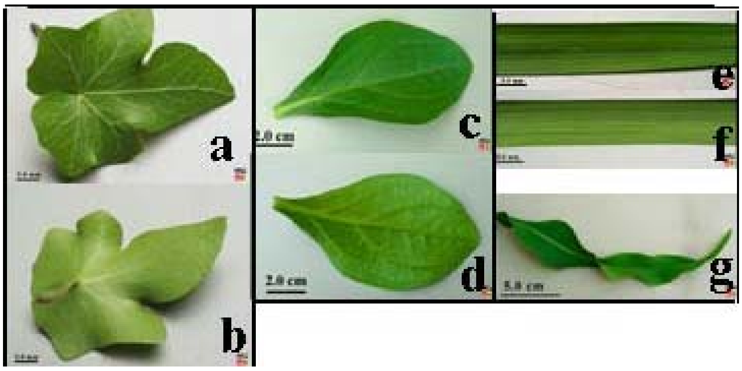


Figure 11. a, c and e. Adaxial views of the leaf of ivy, Petunia and papyrus. b, d, and f. Abaxial views. g leaf of maize.

The side of the leaf turned towards the sunlight is commonly called the upper side. But what is then the true upper side in a twisted leaf like the corn leaf shown in Fig. 12 g?

From an anatomical point of view, the orientation of the xylem and phloem are a point of reference, which is related to the fixed position of these vascular elements in the stem (in Fig. 12: xylem red, oriented toward the inner side in the stem; phloem blue, oriented toward outer side in the stem).

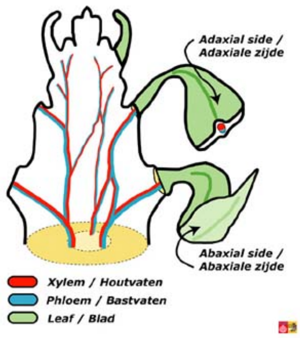


Figure 12. Diagram of the orientation of the adaxial and abaxial side of a leaf with respect to the xylem and phloem in the vascular bundle.

It is therefore more accurate to use the terms adaxial to indicate the side of the leaf most close to the xylem, and the term abaxial for the side facing the phloem (Fig. 12).

2.3.4. Supporting tissue (sclerenchyma and collenchyma)

Mechanical strength is provided to the leaf by sclerenchyma and collenchyma cells (Fig. 13). What is the difference between the sclerenchyma and collenchyma? Sclerenchyma cells (from the Greek skleros = hard and enchyma = infusion) are thick-walled, mostly lignified cells that enable the surrounding softer tissue to withstand various strains. They are often found close to vascular bundles, in particular at the base of the midrib vein. Sclerenchyma cells show much variation in shape, but are often grouped into fibres (elongated cells) and sclereids (Fig. 13 c), which are relatively shorter than fibres. Collenchyma cells also have an explicit thick wall and appear in variable forms, but they are living cells in contrast to mature sclerenchyma cells.

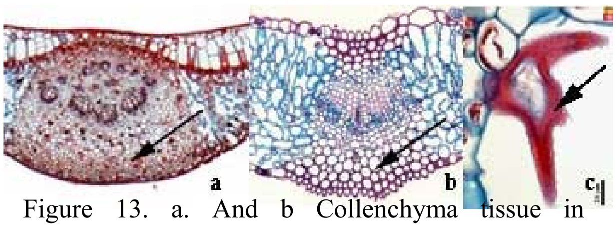


Figure 13. a. And b Collenchyma tissue in respectively ivy and lilac. c. Sclereid in water lily.

3. Taxonomical variations

Historically, living organisms have been divided in taxonomical groups on account of morphological and anatomical characteristics. More recently, biodiversity and phylogeny have been reviewed with the benefit of advances in molecular genetics and the developments in bio-informatics. However, both approaches to classify the monocots and the dicots (the two subgroups of the angiosperms (= Anthophyta = flowering plants) are consistent when we regard the leaf architecture. In the next pages we are going to address the question: what are typical features of the leaf anatomy of a monocot and a dicot plant?

3.1. Characteristics of leaves of dicots

Leaves of dicots may be indented, like in ivy (Fig. 14 a), or show a compound structure, like in tomato (Fig. 14 b). The major venation is feather-like (Fig. 21b for Petunia) or hand-like (Fig. 14c for ivy), the minor venation net-like. Epidermal cells resemble puzzle pieces (Fig. 14 d and e for Petunia), and the stomata are oriented in all directions (Fig. 14e).

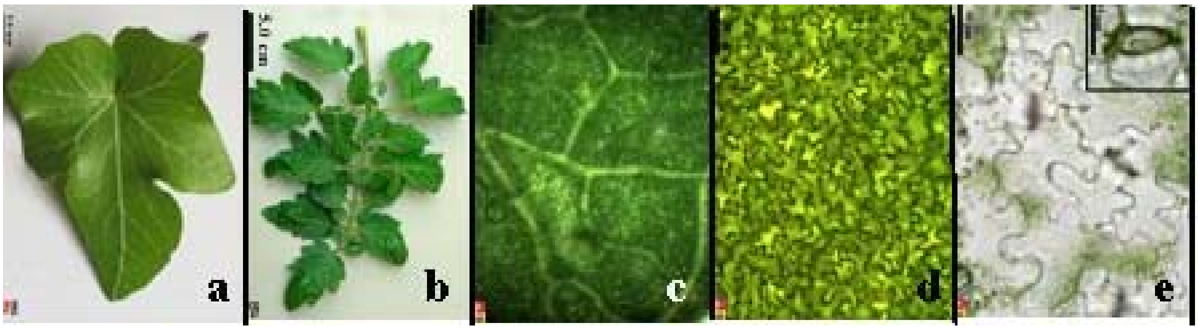


Figure 14. Characteristics of leaves of dicots: ivy in a and c, tomato in b and Petunia in d and e. a. Indented morphology. b. Compound leaf (only 1 leaf!). c. Reticular venetion. d. Puzzle-shaped epidermal cells. e. Criss-cross oriented stomata.

3.2. Characteristics of leaves of monocots

Leaves of monocotyledonous plants are mostly arrow or band-shaped and show a parallel venation. The epidermis cells, including the stomata, are almost always arranged in parallel arrays. Examples of monocots are maize (family of the Graminae; Fig. 15 a-d) and papyrus (family of the Cyperaceae; Fig. 15 e-h)

3.3. Leaf formation

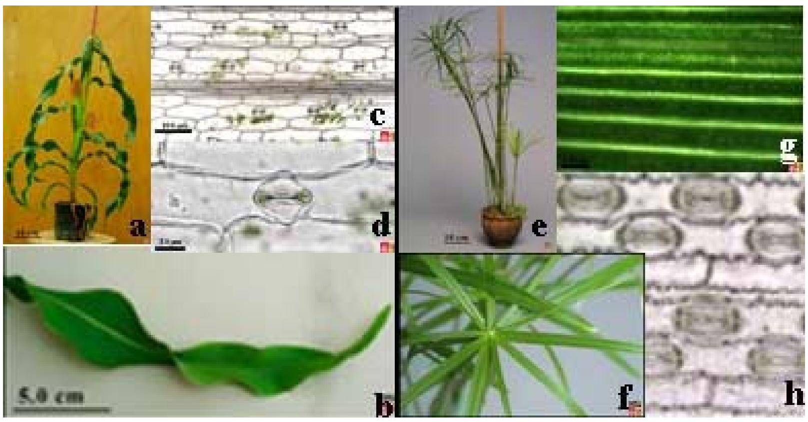


Figure 15. Characteristics of the leaf of monocots. a-d Maize. e-h. Papyrus. Notice the band shape of the leaf (b and f), the parallel ventation (g) and the linear arrangement of the stomata and epidermal cells (c, d and h).

3.3.1. Initial stage

How are leaves formed? Although variations in morphology exist between the shoots of monocot and dicot plants, the initial stages of leaf formation are similar:

Leaf formation starts immediately behind the top meristem (Fig. 16; 1) with periclinal (new cell wall parallel with the surface; expansion cross to surface) divisions in the cell layers under the epidermal layer (Fig. 16; red in 2). After the first divisions also anticlinal (new cell wall at right angles to the surface; expansion parallel to surface) divisions occur the epidermis as well as in the layers underneath (Fig. 16; blue in 2). The result is a small bulge (Fig. 16; 3) that will further develop into a leaf. From this point on, leaf growth differs between monocots and dicots.

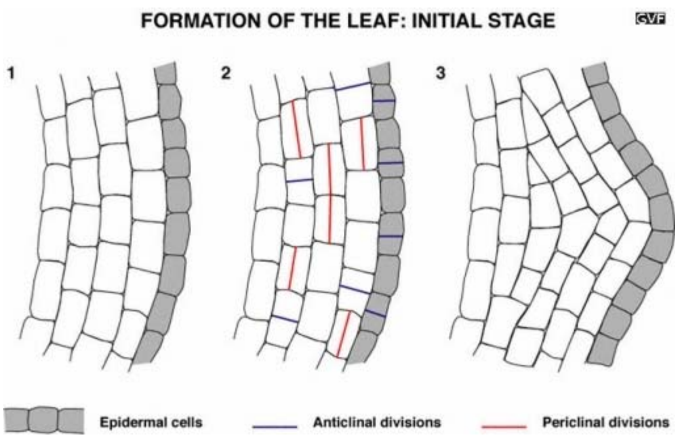


Fig. 16. Initial stage of leaf formation for both monocots and dicots.

3.3.2. Leaf formation in dicots

The development of a dicot leaf continues as follows:

The initially formed bulge further elongates by cell divisions throughout the bulge (Fig. 17; 1-5). Next, at the top of the extended bulge, cells start to divide a single plane causing the bulge to broaden (Fig. 17; 6). Depending on the species, division activity may decrease or increase in distinct locations in the leaf, leading to the diversity in morphology known from dicots (Fig. 17; 7-9). The lower part of the extended bulge will develop into the leaf stalk or petiole (Fig. 17; 9). In further courses students learn about how such developmental steps are regulated at the molecular level.

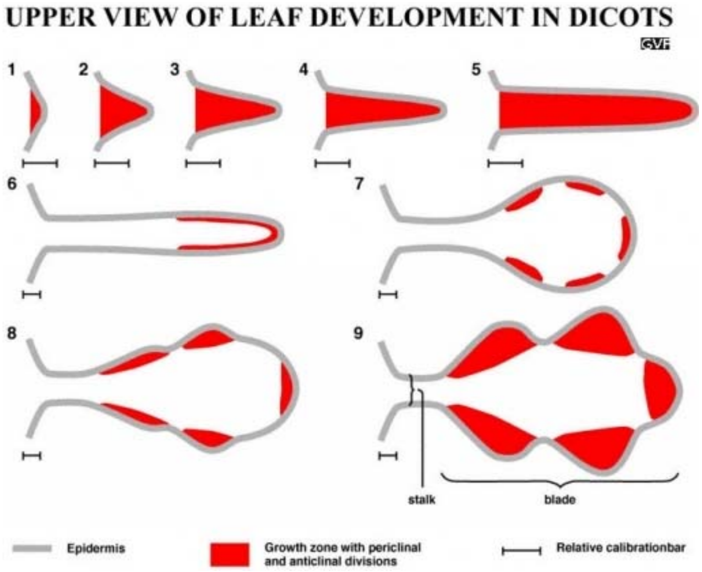


Figure 17. Leaf formation in dicots. Red areas represent growth zones with periclinal and anticlinal divisions

Images of the process of leaf formation in a dicot are shown in Fig. 18 for *Coleus sp.*

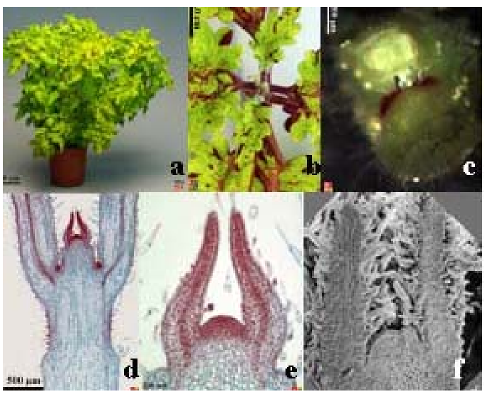


Figure 18. Leaf formation in *Coleus sp*. a. Habitus. b. Upper view of the apical meristem. c. Dissected apical meristem. d. longitudinal section through the tip of the stem in which the base of leaves can be seen. e. Light microscopical view of the apical meristem and initial region of leaf formation. f. Scanning electron microscopy of a similar region as in e.

3.3.3. Leaf formation in monocots

In monocots the initial bulge (Fig. 16) further elongates by periclinal and anticlinal cell divisions occurring in one plane (Fig. 19; red area in 1-5). Next, a division zone (Fig. 19; blue band in 6) gives rise to the leaf sheath (Fig. 19; light green in 7) and the leaf blade (Fig. 19; dark green in 7). The leaf further expands by stretching of the cells (expansion parallel to the leaf long axis). Figure 20 shows the morphological and anatomical views of leaf primordia in the monocot pondweed.

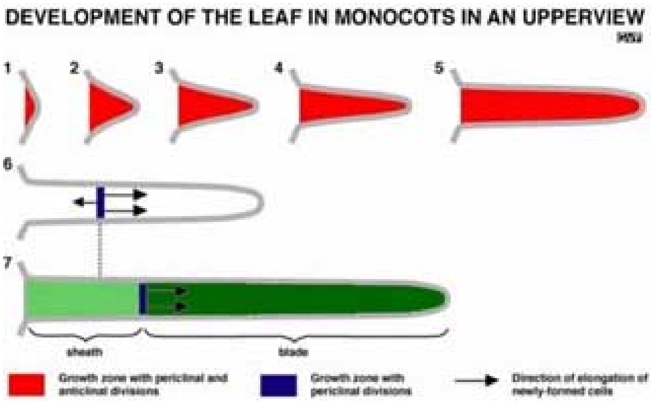


Figure 19. Diagram of leaf formation in a monocot. Red areas represent zones of periclinal and anticlinal divisions. The blue stripe depicts the zone where cell division and elongation occurs in the same direction as the arrows. Light green: leaf sheath. Dark green: leaf blade.

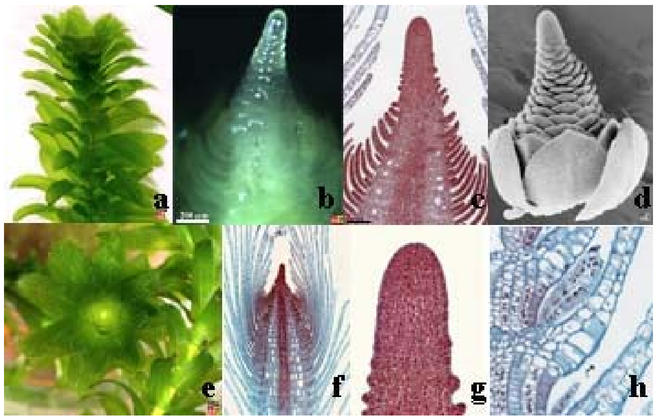


Figure 20. Images of leaf formation in a monocot: *Elodea canadensis* (pondweed).
a. Habitus
b. Dissected stem top with leaf primordia
c. Long section through tip with leaf primordia
d. SEM view of tip
e. Close-up of leaf bud
f. Overview of tip in longitudinal section
g. Detail of first onset for leaf formation
h. Detail of base of leaves in longitudinal section.

4. Anatomical adaptations to the environment

Plants have developed astounding strategies to maintain photosynthesis and inter transport of water and nutrients under various ecological conditions. In particular leaves show far-reaching adaptations that enable them to survive in a hostile environment and to deal with attacks of predators and parasites. In which respects would leaves of marsh plants different from those of desert plants?

4.1. Leaf of mesomorph plants

Plants living in a to a moderate climate with regular rainfall have so-called mesomorph characteristics. They do not require extreme protection, but still need to be able to cope with periods of drought or coldness. The physiological conditions in winter may be so critical that many (but not all) mesomorph plants shed their

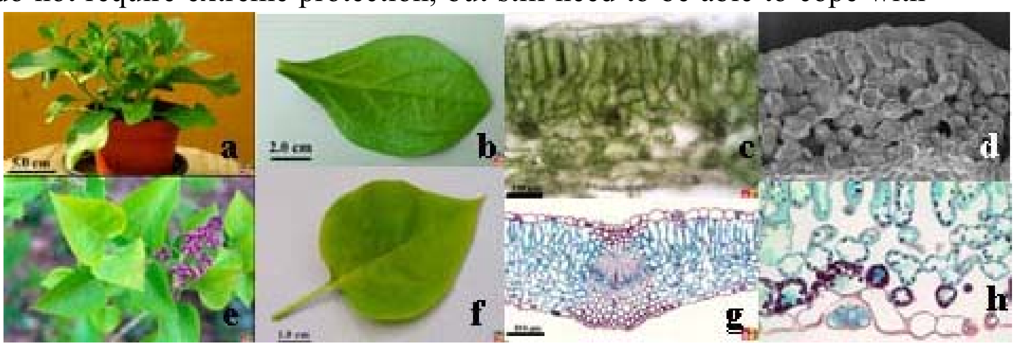


Figure 21. Mesomorph plants; leaf characteristics in Petunia (upper panel) and lilac (lower panel)

leaves in fall and make new lobe in spring. Examples of mesomorph species are petunia (Fig. 21 a-d) and lilac (Fig. 21 e-h). They do not require extreme protection, but still need to be able to cope with periods of drought, darkness and coldness. Their physiology is coupled to seasonal variations. They roughly follow a global annual rhythm of strong growth in early spring, flowering in late spring and summer, seed formation in late summer and fall and rest or death in winter. Under influence of hormones many but not all mesomorph plants shed (abscission) their –old- leaves (senescence = aging) in fall to make new lobe in spring. Such plants are called deciduous plants. Events marking abscission are the development of tyloses, balloon-like extensions of a parenchyma cell that protrudes into the lumen of xylem vessels and plug them, and the formation of sclerenchyma. After leaf shedding the wound is sealed by callose deposition and a periderm that replaces the epidermis (No photos yet).

4.2. Leaf of xeromorph plants

Plants in arid regions have leaves with xeromorphic characteristics (xeros = dry in Greek). These plants are able to absorb sufficient amounts of water from the soil, thanks to deep roots or rapid accumulation in tissues. They retain the water effectively and prevent desiccation through the dry air. Moreover, they are able to sustain high levels of solar radiation. Look at Fig. 22 to get an impression of xeromorphic adaptations of the leaf. These include a thick cuticle and a multi-layered epidermis with few stomata that are located in the lower epidermis only. Additional adaptations involve the development of uni- or multicellular hairs and the occurrence of the stomata in a sunken chamber (cryptomeric stomata).

Figure 22. Xeromorphic characteristics in the Mediteranean shrub Oleander (a. Habitus) and American privy (e. Habitus). c. Cryptomeric stomata and hair protection. d and g . Multilayered epidermis covered by a thick cuticula.

Sometimes, other cells but the guard cells partake in opening and closing of the stomata and create a kind of anti-chamber to minimize water lost through the stomata. Such a "double door" system can be observed in privy (Fig. 23).

Figure 23. Guard cells and subsidiary cells corroborating the enclosing and opening mechanism of a stoma in privy. The ledges of the subsidiary cell create a kind of anti-chamber that effectively prevents excessive water lost through the stoma.

The needles of the gymnosperms such as the pine tree (*Pinus sylvestris*) are in fact also leaves (Fig. 24). They show xeromorphic characteristics and a linear alignment of stomata, which resembles the arrangement of a taxonomically completely different group, i.e.

Figure 24. Needles of pine (a Gymnosperm). a. Needles and cones. b. Cross section through a needle c detail of a resin duct. Resin deceives potential enemies. d. Linear alignment of the stomata. e. Detail of stoma.

the monocots (belonging to the angiosperms = anthophyta = flowering plants).

Some plants, for example ivy (*Hedera helix*), combine mesomorphic with xeromorphic characteristics like leathery leaves with a compact architecture (Fig. 25). This ambivalent behavior may be exaplained by the fact that this evergreen sometimes grows in a relatively humid, woody and shady environment, but that it has as well to manage with the stress of winter and exposure being a covering plant.

Some plants combine xeromorphic and mesomorphic characteristics, like for example the ivy (*Hedera helix*) (Fig. 25). Ivy grows in relatively humid, woody and shady environments. However, it is an evergreen that carries its leaves throughout the relatively challenging winter. Thus, though its largely built as a mesomorphic leaf, it has a leathery surface and its tissues are very compact. Another particularity of ivy is that it adapts the number of layers of palisade parenchyma to the availability of light.

Figure 25. Thick-walled epidermis cells and thick cuticula in ivy.

4.2.1. Succulents - CAM plants

To survive in a dry environment with little and irregular rainfall, plants may combine xeromorphic trends, with metabolic adaptations (particularly Crassulacean Acid Malate metabolism or CAM; Fig. 27, and with the storage of water in their leaves and other parts of their body. Plants using water storage in their body are called succulents. Well-known succulents are the pot plant jade plant (*Crassula ovata*; Fig. 26) and Euphorbiaceae. The chlorenchyma cells get a swollen appearance and their central vacuole can become very large. The differentiation between palisade and spongy parenchyma is not clear or even inexistent. To prevent water loss, the stomata of CAM plants like jade plant, are closed by day, and open only at night to absorb CO_2, when the temperature decreases and humidity rises. However, as we have seen in paragraph 2.1., light is required for the CO_2 fixation, while it is dark at night! How do CAM plants resolve this timing problem? These plants have evolved a mechanism to accumulate CO_2, the source of carbon, as malate in their large vacuoles. Malate is released later, during day, to be used for the light-dependent photosynthetic reactions. The so-called CAM metabolism was discovered in Crassulacean plants, but it appears to occur also in dicot plants, and in a number of monocots, among others the crop pineapple and the pot plant Sansevieria.

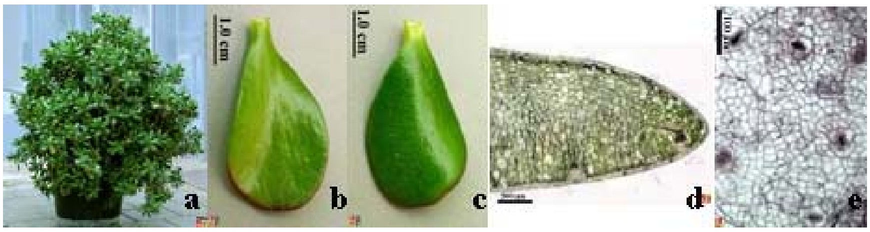


Figure 26. Jade plant, a typical succulent in which water is stored in parenchyma cells. e. Waxy layer on the surface of the leathery leaf.

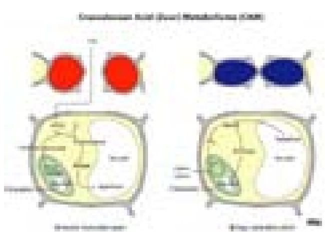


Figure 27. CAM principle.

4.3. Leaf of hygromorph plants and water plants

Which characteristics would you expect in leaves of marsh and riverbank plants and true water plants? Hygrophytes (hygros = water in Greek; phyta = plant) is the name given to plants from a humid and shady environment with an ample supply of water.

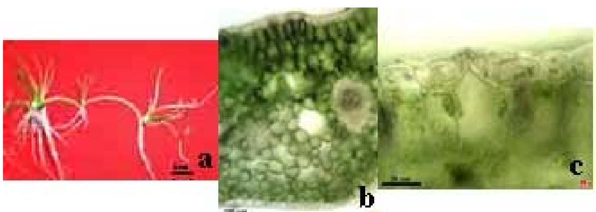


Figure 28. Hygromorph characteristics in *Ranunculus reptans* and *R. flammula. a*. Habitus. b. Cross section through the leaf showing stomata on the adaxial as well as abaxial side. c. Protruding stomata and outermost thin cuticle.

They possess so-called hygromorphic leaves with a single epidermal layer, a thin cuticle, often protruding guard cells, and reduced supporting tissue. Examples of such hygrophytes are the creeping spearworts (Fig. 28; research: www-eco.sci.kun.nl/expploec).

Plants with floating leaves (Fig. 29 a, b) thank their buoyancy to large air cavities in the sponge parenchyma (Fig. 29c). They obviously do not lack water. However, such leaves are exposed to intense sun radiation and therefore often show a protective cuticle (Fig. 29 e). In contrast to most terrestrial plants, the stomata in floating leaves are present at the top only (Fig. 29 e) to facilite gas exchange. Along with the availability of ample sunlight and water the palisade parenchyma is well developed Fig. 29 d). Large air canals (aerenchyma) allow oxygen to diffuse from the leaf to the stem and the root.

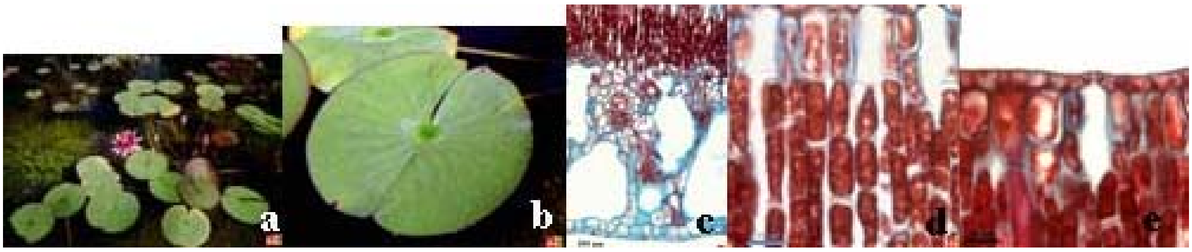
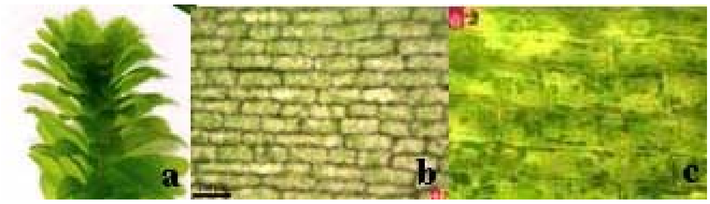


Figure 29. Characteristics of leaves floating on the water surface: c. Large intercellular cavities providing buoyancy and contributing to oxygen supply. d. Multi-layered well-developed palisade parenchyma. e. Stomata present on the adaxial side only.

Figure 30. A submerge plant, the Canadian pondweed (*Elodea Canadensis*). The leaves consist of only two layers of photosynthetic active cells. The chloroplasts of these cells exhibit a vivid circular cytoplasmic streaming (c. Animation in the html version).



Completely submerged water plants, like pondweed (Fig. 30), do not need stomata, but exchange carbon dioxide and oxygen directly via the thin, air-permeable cuticle. The epidermis is under-developed or even absent. The leaves are very thin or thread-like to provide the necessary surface/volume ratio. Despite the reduction in supporting tissues, submerged plants can grow upright toward light thanks to large air cavities in the leaf, which provide buoyancy. The water transport system, the xylem, is strongly reduced, as water is plenty available. A palisade parenchyma is absent, since the intensity of the sunlight is relatively low under water.

4.4. Modifications of economical significance

Thickened leaves serve in some species as storage organs of starch and other nutrients, that help the plant to overcome difficult periods, in particular winter monthes. Sometimes, the leaf tissues contain also substances that have a special taste or smell that will either attract or repel animals. Humans have selected and breeded plants with such properties to obtain valuable products.

Examples of leaves with an economical significance are spices (e.g. laurel, tea), medicinal plants (e.g. *Aloe vera* or wild quinine, *Parthenium integrifolium*), ornamental bulbs (e.g. tulips) and edible bulbs of the genus Allium (e.g. onion, garlic, shallot, chives, leek).

http://www-vcbio.sci.kun.nl/eng/virtuallessons/leaf

In some vegetables the leaf blade is the most important part for consumption, like in spinach and cabbage, whereas in other crops the leaf stalk constitues the actual food product, like in rhubarb and fennel (fenkel).

Figure 31. Epidermal cells in the modified leaves of onion scales.

(Note that the epidermal cells of onion bulbs, an example of modified leaves, are funny and illustrative objects for studying organelle movement or physiological features, like osmosis and plasmolysis; see Fig. 31 and image-film gallery: http://www-vcbio.sci.kun.nl/image-gallery/search).