XI. LEAVES

Bot 404—Fall 2004

A. Leaf Morphology

1. Definitions

   -<u>leaf</u> = a determinate lateral appendage in the axil of which a branch (bud) is produced

   -<u>node</u> = place on the stem where a leaf is attached

   -some leaves can be indeterminate to a limited extent because of an intercalary meristem

   -some leaves (ferns, angiosperms) appear to be truly indeterminate (exceptions to definition or are they really leaves?), either because of apical activity or because of 2° growth

2. Functions/modifications

   -the primary function is photosynthesis (but initially may have been for protection of the shoot apex)

   -leaves may also be modified to serve as bud scales, floral bracts (protection of developing inflorescences and/or attraction of pollinators), sepals (protection of flower buds), petals (attraction of pollinators), nutrient storage (cotyledons, bulbs), spines, tendrils, glands, and insect traps

3. Basic gross leaf structure

   a) lamina (or blade)—the flattened portion of the leaf (midrib basically an extension of the petiole)

      -may be simple or variously compound (pinnate, palmate)

      -may have various lobing or serrate patterns on the margin

      -may be lacking entirely

   b) petiole—the "stalk" of the leaf, may be present or absent

      -may be fringed or winged (hard to tell from sessile)

      -may have stipules associated with it

      -leaves of many monocots appear to have no lamina, only a flattened elongate petiole

4. Epidermis (previously discussed)

   a) cuticle

      -often more prominent on leaves than on stem

      -different patterns, thicknesses

   b) epidermis

      -derived from protoderm

      -single or multiple from protoderm divisions

      -includes epidermal cells, guard cells, subsidiary cells; other specialized cells include: cork, silica, bulliform, sclerenchyma

      -adaxial surface usually with few stomata, abaxial surface with many

c) trichomes

-essentially any outgrowth of the epidermis, a plant hair
-glandular or not, uniseriate, multiseriate, branched or not
-additional discussion under trichomes and secretory structures

5. Venation
   1. Petiole

      -frequently stemlike in organization
      -leaf traces enter petioles and may remain separate or variously fuse and rebranch
      -vascular arrangement may change from base to apex of petiole

   2. Midrib

      -extension of the petiole in terms of vascular tissue
      -the midrib itself is usually distinct from the lamina and often protrudes on one or both sides; also can contain > 1 bundle
      -if one bundle is larger it is called the midvein
      -vascular bundles will depart variously from midrib into the lamina

   3. Lamina

      -major venation patterns in vascular plants

      a) dichotomous

      -<u>open dichotomous</u>—no dominant bundles, and they repeatedly divide into two equal veins throughout; veins end in the margin
      -found in pteridophytes, many gymnosperms, two dicots
      -<u>modified open dichotomous</u>—there are more or less dominant bundles (midvein) but the branching units are dichotomous; derived from open dichotomous through fusion of basal portions, essentially a pseudomidrib
      -sometimes branches of the dichotomy fuse to form a primitive reticulation (network)
      -found in many ferns

      b) single midvein

      -essentially all the venation is reduced to a single bundle (or maybe 2) running the length of the lamina
      -found in many needle-leaved conifers and in angiosperms with reduced leaves (e.g., in specialized habitats such as very dry or very wet habitats)

      c) parallelodromous

      -parallel veins; major veins run for virtually the full length of the leaf, essentially parallel but they meet at the tip
      -small veins (called commissural veins) connect the major parallel ones; common in monocots

d) reticulate

-veins form a network (= net-veined)

-both major and minor veins present

-widespread in angiosperms, but also found in some ferns and the Gnetales (a group of gymnosperms)

-<u>areole</u>—smallest area bounded by vascular bundles

-<u>vein endings</u>—extensions of bundles into areoles; present in most dicots but absent in most monocots

-basically, in leaves with reticulate venation, every mesophyll cell is within 6 cells of a vascular bundle

-two subtypes of venation:

<u>craspedodromous</u>—marginal; major veins extend right to the margin; craspedo- = marginal and –dromous = course

<u>camptodromous</u>—flexible; major veins approach the margin but bend before they reach it; may form loops; campto- = flexible

B. Angiosperm Leaves

-representative terrestrial dicot leaf (DIAGRAM)

1. Basic anatomy

   -can think of the basic leaf as a sandwich, with the bread being the upper (adaxial) and lower (abaxial) epidermises, and the filling being the middle tissue (mesophyll = middle leaf)

   -from top to bottom, the five layers and sublayers are lettered a-e

-chlorenchyma—term is used for the photosynthetic tissue (spongy and palisade mesophylls; also known as spongy and palisade parenchyma)
-leaves of gymnosperms, dicots and monocots are basically very similar (and also fern leaves) in internal structure

a) Adaxial epidermis

-usually with few or no stomates but there are many exceptions especially in plants with vertical leaves, floating leaves, or leaves in very shady habitats
-may be multiseriate (multiple epidermis)

b) Palisade mesophyll

-palisade = pickets in a fence
-the cells are elongated, cylindrical and regularly arranged in 1-5 rows (as seen in leaf XS)
-in vertical leaves, the layer may not be distinguishable OR it may occur below both epidermal layers
-cylindrical shape thought to be most efficient for a cell that is intercepting intense light; also, cells are slightly separated giving a large surface area for absorbing CO_2
-but, cells can't be separated too widely as spaces provide capillary action for water distribution

c) Vascular tissue

-xylem always toward the adaxial surface, phloem toward the lower surface; consequence of their relative positions in the stem and collateral bundles passing into the leaves
-larger bundles rarely may undergo a small amount of 2° growth; smaller veins and minor venation 1° only
-larger bundles usually lack a parenchyma bundle sheath, or there is a sclerenchyma sheath, but xylem is not in contact with air spaces
-smaller veins usually have a parenchyma sheath that tightly surrounds the bundle, even around the vein endings = bundle sheath
-bundle sheath relatively inconspicuous in most species (related to C_3 photosynthesis)
-bundles sheath with enlarged cells in C_4 species (part of kranz anatomy, or kranz syndrome)
-sheath insulates the bundle from the atmosphere of the leaf; prevents air from reaching the xylem
-compared by some to an endodermis, and in fact the sheath may have a casparian strip in ferns, conifers and some dicots (may prevent water from moving back into the bundle from the lamina)
-may be bundle sheath extensions to one or both epidermises; ad- and abaxial extensions may be parenchymatic or sclerenchymatic (fibers)

d) Spongy mesophyll
- -one to several "layers" at and below the vascular bundles
- -cells are usually irregular in shape
- -large intercellular air spaces are usually present; apoplast typically larger than the symplast
- -always an air space (substomatal chamber) associated with a stomate
- -concentration of chloroplasts is lower here than in palisade mesophyll

e) Abaxial epidermis
- -commonly with most or all of the stomates
- -may be multiseriate

2. Comparison of dicot and monocot leaves

-leaves exhibit many adaptations to different habitats, so leaf morphology and anatomy is variable in both dicots and monocots

a) Dicot leaves
- -usually craspedo- or camptodromous venation (vein endings usually present but lacking in a few groups, e.g., *Acer*, sunflower family)
- -if parallelodromous, then always with vein endings
- -margins linear to serrate, highly variable
- -palisade layer often developed
- -usually lacking a sheathing base (but this present in carrot and aralia families, e.g.)
- -petiole present or absent

b) Monocot leaves
- -usually parallelodromous, margins usually linear (not serrate but can be lobed) but some have true reticulation
- -usually lacking vein endings, even if venation seems to depart from parallel
- -usually lack palisade layer (homogenous mesophyll)
- -usually with a sheathing base; a petiole-like structure (pseudopetiole) can be present between sheath and blade
- -intercalary meristem often present at base of blade in taxa with straplike blades

3. Specializations

a) aquatic plants (hydrophytes)
- -leaves almost always reduced in complexity because water supports them and no need to prevent drying out
- -little xylem (can be just a single vein) or sclerenchyma but fibers do help to protect against tearing; cuticle minimal
- -floating leaves typically have stomates on the adaxial surface
- -submerged leaves are usually finely dissected or very thin and cylindrical
- -gas spaces are common in leaves, stems, and roots; in leaves and upper

stems useful in support (remaining upright) but also allow gas exchange throughout (even down into the roots)
-most aquatic angiosperms have an endodermis in the stem and leaves—keeps water confined to xylem so that water doesn't get into gas spaces
-transpiration is usually absent, so water flows through plant due to root pressure

b) xerophytic plants
-adaptations to conserve water and reduce intense light
-e.g., thick cuticle, multiseriate epidermis, stomatal crypts, abundant trichomes
-stomatal crypts—areas where stomata are restricted to pockets in the epidermis (reduces the moisture gradient)
-may also exhibit CAM photosynthesis, in which the stomates open at night
-some tendency to be isobilateral

c) sun/shade leaves
-differences in tissue occur in leaves from the crown vs. interior
-sun leaves thicker, thicker cuticle, more cell layers

4. Grass leaves
-are typical monocot leaves in general
-exemplify the anatomical features associated with C_3 and C_4 photosynthesis
-C_3 is the common condition in plants
-C_4 has evolved in a number of families, notably the grasses and the Chenopodiaceae-Amaranthaceae alliance, among others

1) C_3 anatomy
-*Poa* as an example
-mesophyll with large intercellular air spaces, cells in no special arrangement
-outer bundle sheath cells not enlarged, lacking chloroplasts
-CO_2 is fixed in the spongy mesophyll cells and the Calvin cycle takes place there too (starch produced in mesophyll cells)
-photorespiration occurs when O_2 competes with CO_2 for Rubisco
-generally no disadvantage under lower temperatures, lower light levels and/or sufficient water

2) C_4 anatomy
-corn (maize) or grama grass (*Bouteloua*) as examples
-mesophyll cells usually tightly packed, few or no intercellular spaces
-mesophyll cells often, but not necessarily, radially arranged
-outer bundle sheath cells enlarged, containing chloroplasts, sclerenchyma sheath usually absent except around primary bundles

-closer vein spacing (veins separated by 2-4 cells)
-kranz anatomy refers to the radiate mesophyll; not all C_4 grasses (or other plants) have kranz anatomy
-CO_2 is fixed in the spongy mesophyll cells into a 4-C acid, and transported to the bundle sheath, where Calvin cycle takes place (starch produced in bundle sheath cells)
-allows compartmentalization to exclude O_2 so photosynthesis is more efficient
-generally more efficient under higher temperatures, higher light, and/or less water

C. Gymnosperm Leaves

1. Variation
   -open dichotomous venation most common (e.g., gingko)
   -single midvein common among conifers (reduction from open dichotomous)
   -reticulate pattern only in *Gnetum*
   -leaves range from broad leaves to needle leaves to compound leaves but general structure similar to dicot leaf (except for lack of minor venation)
   -often large areas of mesophyll distant from a vein

2. Unique features
   -gymnosperms (except for *Gnetum*) lack minor venation
   -have two other features instead: transfusion tissue and accessory transfusion tissue
   -<u>transfusion tissue</u>—a mixture of short tracheids (transfusion tracheids) and parenchyma (transfusion parenchyma) lying in a seemingly disorganized way on each side of (around) the true vascular bundles
   -<u>accessory transfusion tissue</u>—found in some conifers; occupies middle plane of leaf between transfusion tissue and margin; consists of elongate accessory transfusion tracheids and elongate accessory transfusion parenchyma (may be analogous to phloem)

3. Needles
   -conifers with needle-like leaves have an endodermis around the vascular bundle (although lacking a true casparian strip) and
   -mesophyll often consists of rosette cells (with lobes); under drought conditions can fold in on themselves (flexible)
   -but some have a mesophyll differentiated into palisade and spongy layers
   -epidermis and layers below are sclerenchyma fibers which maintain the leaf shape during drought conditions (e.g., lack of rain, winter)
   -lipid reserves are built up in the mesophyll during winter; lower freezing point and are hydrophilic

D. Leaf Development

1. Initiation and growth

-simple dicot leaf as representative of the developmental pattern

a) leaf primordium initiates by localized divisions in tunica and varying layers of corpus on flank of shoot apex
-phyllotaxy determines pattern of initiation (e.g., alternate vs. opposite leaves, type of spiral in alternate leaves, etc.)
-leaf initiation is similar in gymnosperms and pteridophytes

b) protoderm divides anticlinally to keep the "skin" expanding
-apical initial in pteridophytes, no distinct protoderm

c) the young primordium has cell division throughout, but once it becomes cylindrical, cell division is more organized

d) lamina develops by local divisions on each flank of the primordium through activity of marginal meristems; thickening is through the activity of the adaxial (ventral) meristem

-a leaf is a primordium until it begins to develop the lamina
-the adaxial meristem (or adaxial thickening meristem) adds cells to the midrib
-the marginal meristem causes marginal growth of the blade (marginal initials) and determines the number of layers in the leaf blade (submarginal initials) (**M**, p. 263; **E**, p. 337, Fig. 18.16)

e) final activity in increasing the length of the leaf is the elongation of the petiole, which is the former basal portion of the primordium in which there was little or no marginal activity
-in many monocots and some dicots which have the general "grass-like" leaf shape, the basal region retains an extended meristematic potential; i.e., it can be stimulated to produce new leaf tissue (intercalary meristem)

f) growth in the blade is accomplished through the plate meristem, which consists of parallel layers of cells that divide only anticlinally to increase the surface area of the blade

2. Differentiation

-on the whole growth ceases first at the apex, so maturation of leaf tissues generally proceeds basipetally (toward the base)

a) epidermis

-initial basipetal wave of stomate formation

-later scattered initiation of new guard cells as leaf expands generally

b) mesophyll

-division ceases first in adaxial epidermis

-division ceases next in abaxial epidermis and spongy mesophyll, although the timing can vary at this stage

-division ceases last in palisade parenchyma

c) vascular tissue (venation)

-procambium differentiates acropetally and continuously

-following this the midvein develops acropetally

-each lateral vein develops from the midvein outward toward the margin, but as a whole they mature basipetally

-minor veins develop generally basipetally and from the margins inward

-in monocots (at least in grasses), the main longitudinal veins and the midrib develop acropetally, whereas the smaller longitudinal veins (----) and the commissural veins develop basipetally

3. Abscission

-mechanism to shed leaves (or other organs) at the end of the growing season or during times of stress (e.g., drought)

-final developmental activity for many leaves

-abscission zone—disc of smaller, more densely staining cells between the vascular bundles and the epidermis at the base of the petiole; two layers:

a) separation (abscission) layer develops as a transverse plate of thin-walled cells

-separation occurs through a) dissolution of middle lamella only or b) dissolution of middle lamella and adjacent cells

-position usually predetermined during leaf ontogeny

b) protective layer formed by deposition of suberin and other substances; cells undergo cell division to form seal; eventually replaced by periderm formed in connection with periderm elsewhere in the stem