Leaf Development

- Several meristems are involved in the development and growth of the leaves.
- They are functioning either simultaneously or sequentially
- These are the apical, adaxial, marginal, plate and intercalary meristems.

- **The variation in leaf form is directly related to the relative activity and duration of the activity of these meristems**
  - **Plants with heteroblastic development: the form of the leaf often changes in a single plant during its ontogeny.**
  - **Plants with homoblastic development: leaf shape remains uniform.**

MERISTEMS

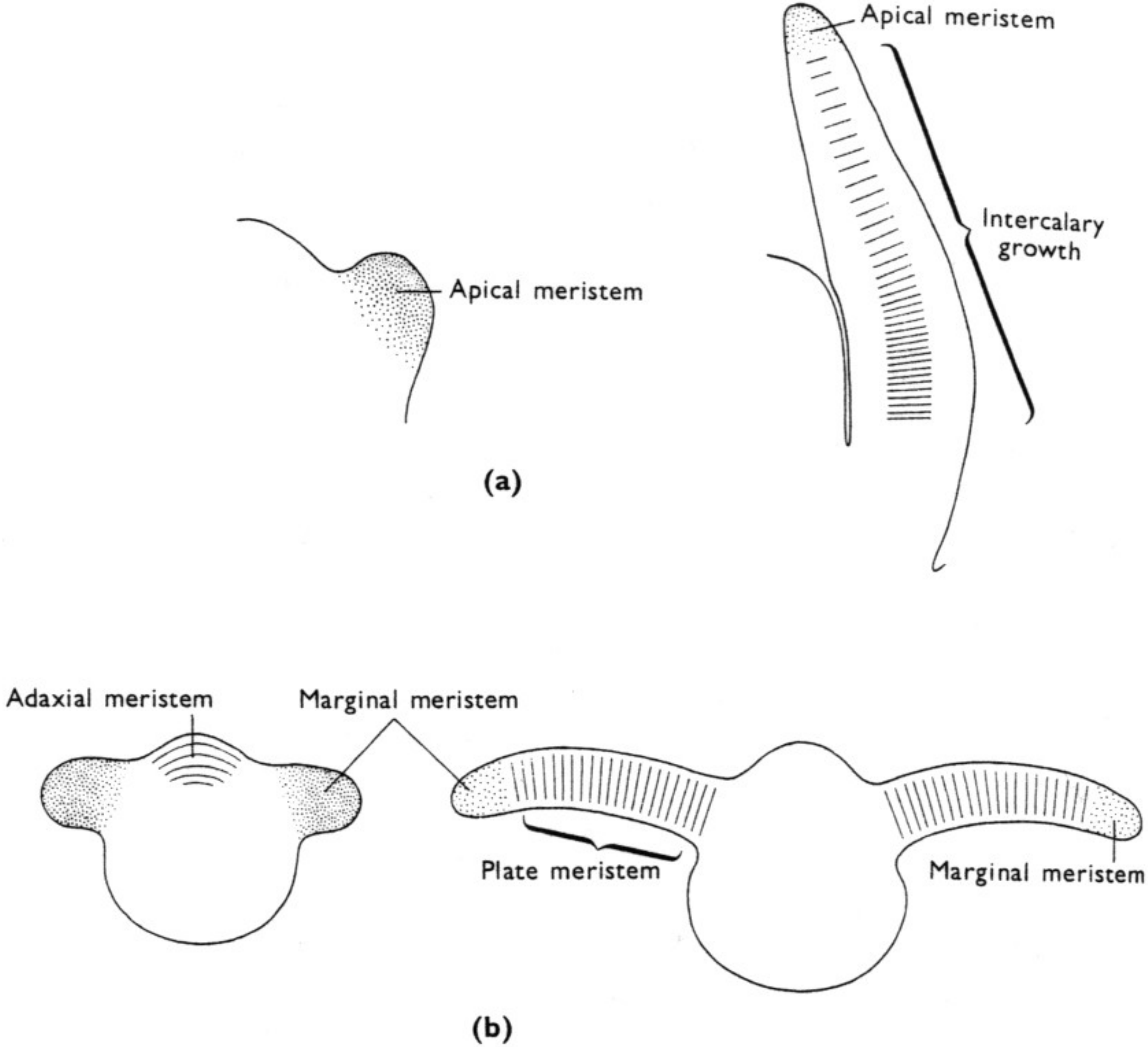


Fig. 5.2 Diagram illustrating the various meristems of a leaf primordium, as seen (a) in longitudinal and (b) in transverse section.

GROWTH HORMONES

- Auxin and gibellerins ➔ stimulate leaf primordia formation
- Protein “expansin” apply to the apical shoot meristem ➔ formation of primordium-like outgrowth. (Remember expansin?...loosening of on the microfibrils, etc…go to your cell wall lecture to refresh this).

LEAF DEVELOPMENT

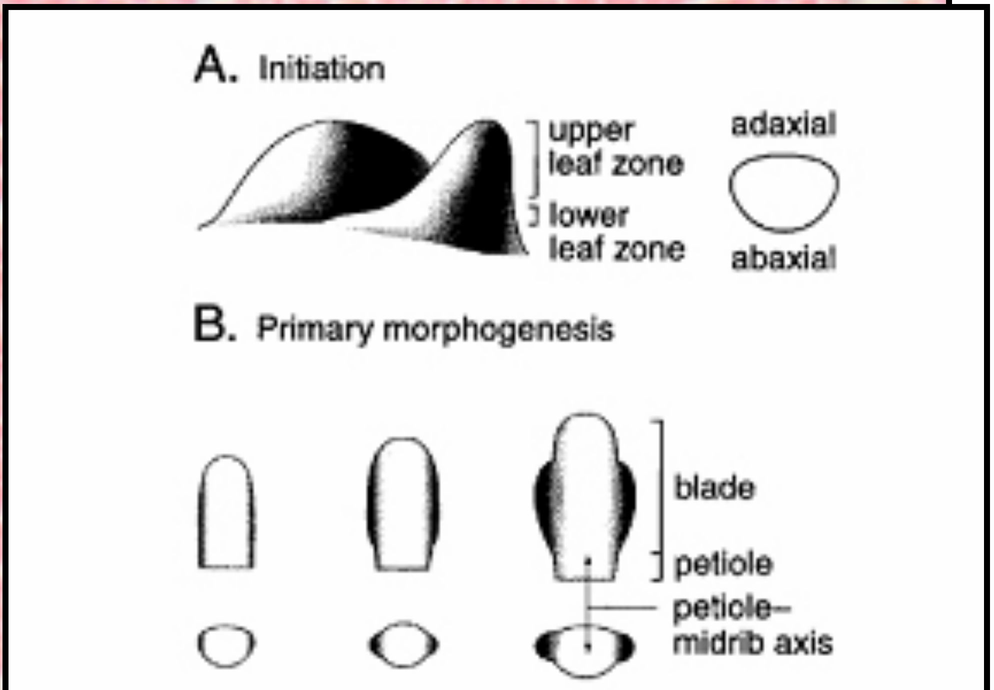
- **A leaf is initiated by periclinal divisions in the peripheral zone of the apical meristem (apical dome)**
- **Successive periclinal and anticlinal divisions ➔originates the leaf primordium (sometimes also called the "leaf primordium buttress").**
- **Localized division in the second layer of cells in the apical meristem**
- **The leaf primodium then grows vertically upward and finally expands laterally.**
- **They are localized and regularly arranged in sites according to the phyllotaxis pattern**
- **Period between the initiation of two successive leaf primordia is known as the PLASTOCHRON or PLASTOCHRONE**

Dicot leaf: 3 phases

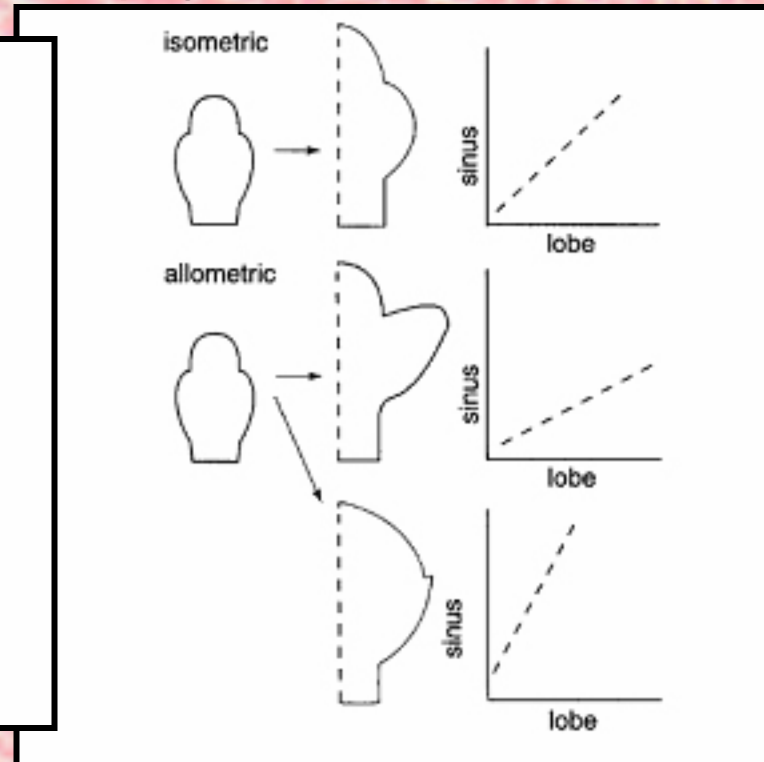
1. LEAF (PRIMORDIUM) INITIATION: initial cell division and cell growth

2. PRIMARY MORPHOGENESIS: formation of primordial leaf axis or phyllopodium (dorsiventral symmetry; petiole and midrib)
   - While increasing in thickness, leaf lamina starts to form outgrowths resulting from cytokinesis in apical and marginal meristems (or marginal blastozones)
   - Continue activity of these meristems ➔ lateral expansion of the lamina, each half extends upward on either side.
   - Compound leaves: marginal meristems become subdivided, each subdivision (leaflet) has its own phyllopodium and apical and marginal meristems.
   - With continuing cell division and cell expansion ➔ entire leaf primordium curves upward.
   - Leaves with petiole (basal meristem)

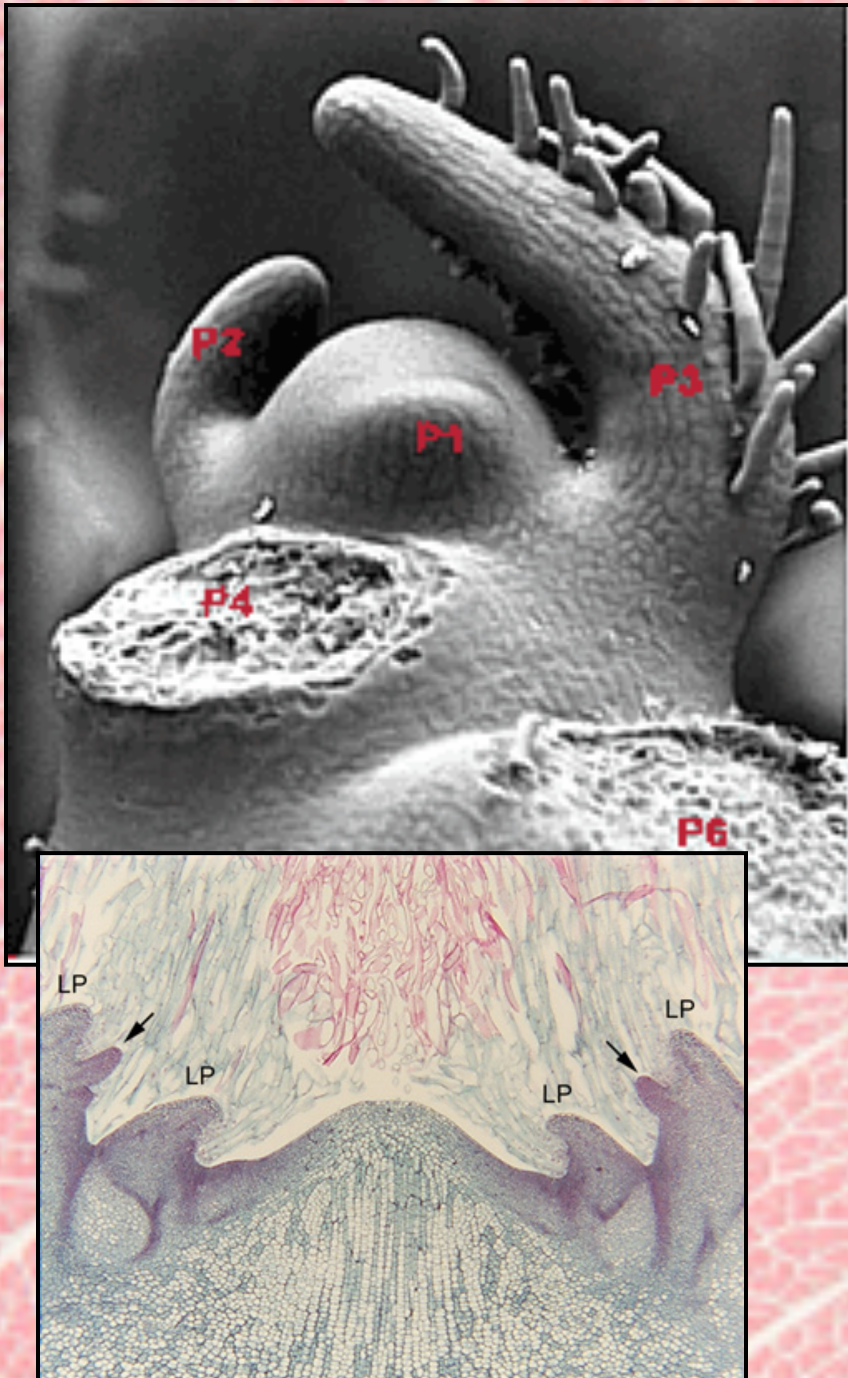
- **3- EXPANSION & SECONDARY MORPHOGENESIS**
  - Longest period in leaf development
  - Leaf continue to grow and differentiate➔ increase in area and volume (95% of the cells)
  - Marginal meristems : 2 layers, short life. Outer layer: epidermis
  - Rest of growth➔ intercalary and diffuse meristematic activity: parenchyma
    - » Mesophyll and provascular tissue
    - » Leaf margin is developed
    - » Basic form: isometric growth
    - » Different morphologies: allometric growth



C. Expansion & Secondary morphogenesis



From dengler and Tsukaya- 2001. Int. J. Pl. Sci. 162: 459-464

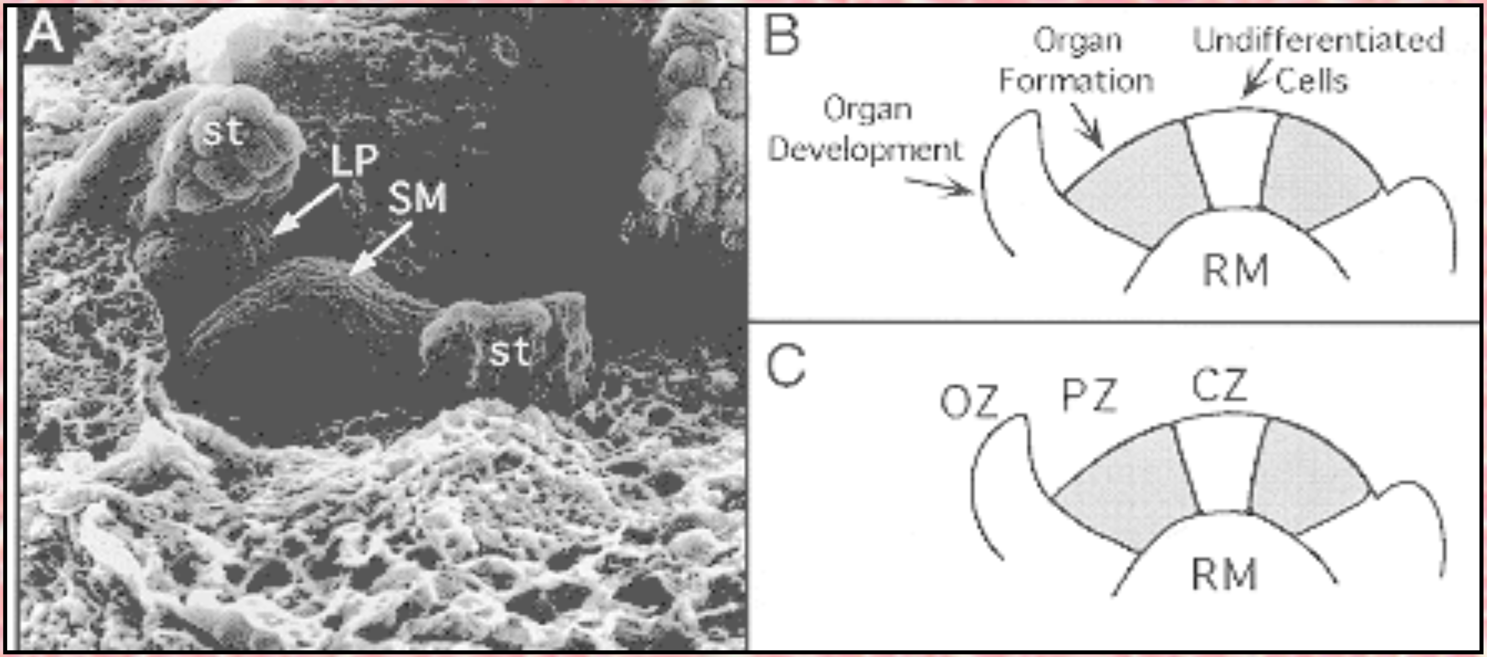


This is a vegetative shoot apical meristem which consists of a small group of dividing cells, they give rise to leaf primordia in very regular and predictable temporal and spatial patterns.

P1-P6 are existing primordia with P1 being the youngest. I1 and I2 are the next primordia to be formed.

SHOOT MERISTEM (SM)

- Maintains pool of undifferentiated cells
- Directs undifferentiated cells toward organ formation and differentiation

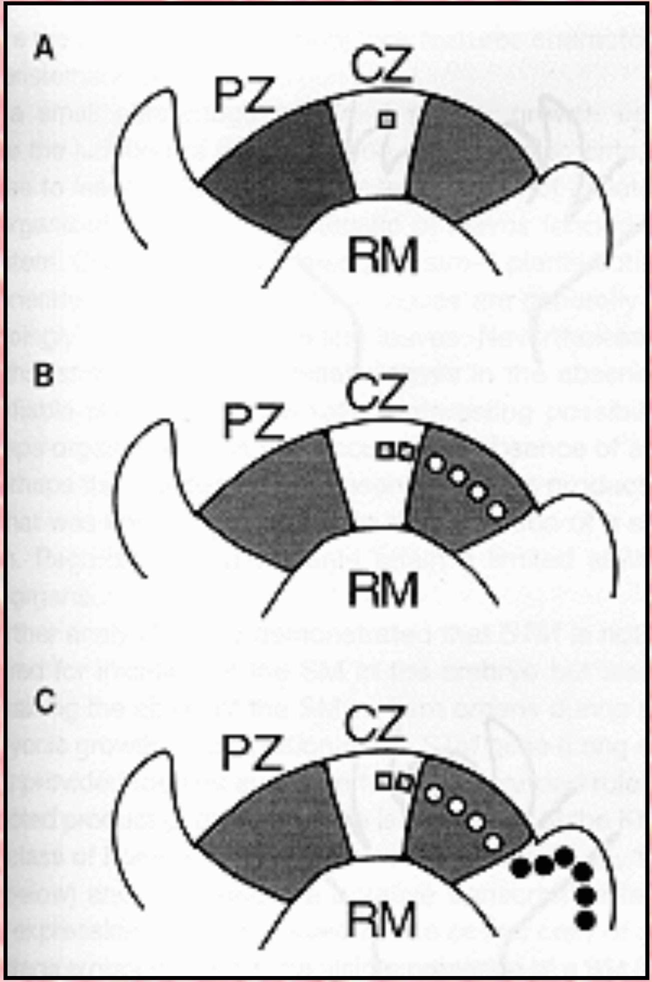


lp - leaf primordium; st - stipule primordium

REGIONS OF THE VEGETATIVE SHOOT MERISTEM

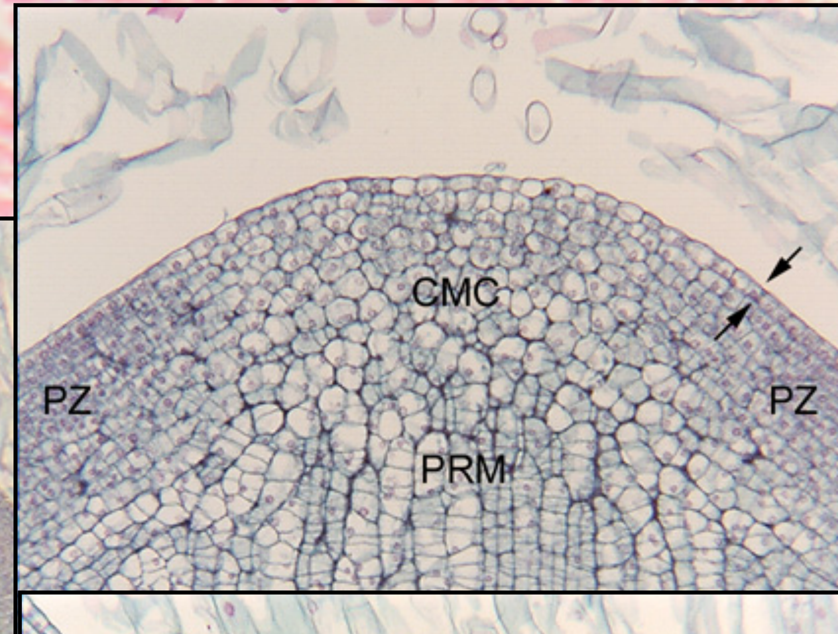
- CZ - Central zone : Center of shoot meristem; low rates of cell division; cells remain undifferentiated
- PZ - Peripheral zone: Surrounds the CZ; rapid rates of cell division; cells can differentiate
- OZ - Organ zone: Site at which organ primordia (e.g.. leaf, flower) become distinct.
- RM - Rib meristem: Gives rise to vascular and interior stem structures

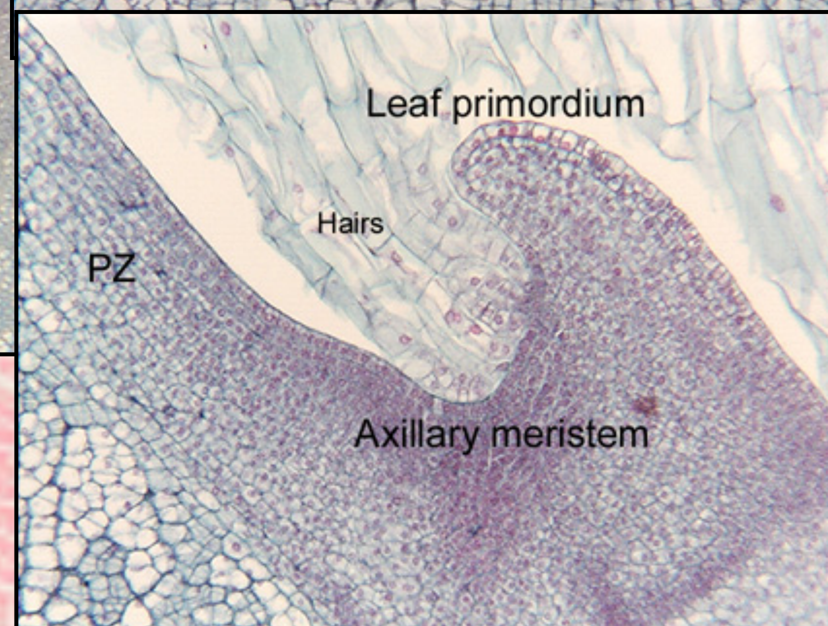
- (A) The CZ consists of undifferentiated cells, which are characterized as being small, and primarily consist of cytoplasm, with only small vacuoles. More importantly, undifferentiated cells retain the ability to initiate any organ type.
- (B) As the SM grows, cells from the CZ are "left behind" to form the PZ. It is thought that positional information in the PZ triggers differentiation into primordia. Once differentiation has begin, cell fate is determined. In other words, cells in the PZ might only be able to differentiate into leaf cells.
- (C) As cell division continues, the older PZ cells begin to develop into discrete primordia (eg. leaf primordia), and are now referred to as OZ cells.



cz: central zone
pz: peripheral zone
rm: rib meristem
sm: shoot meristem

EXAMPLE





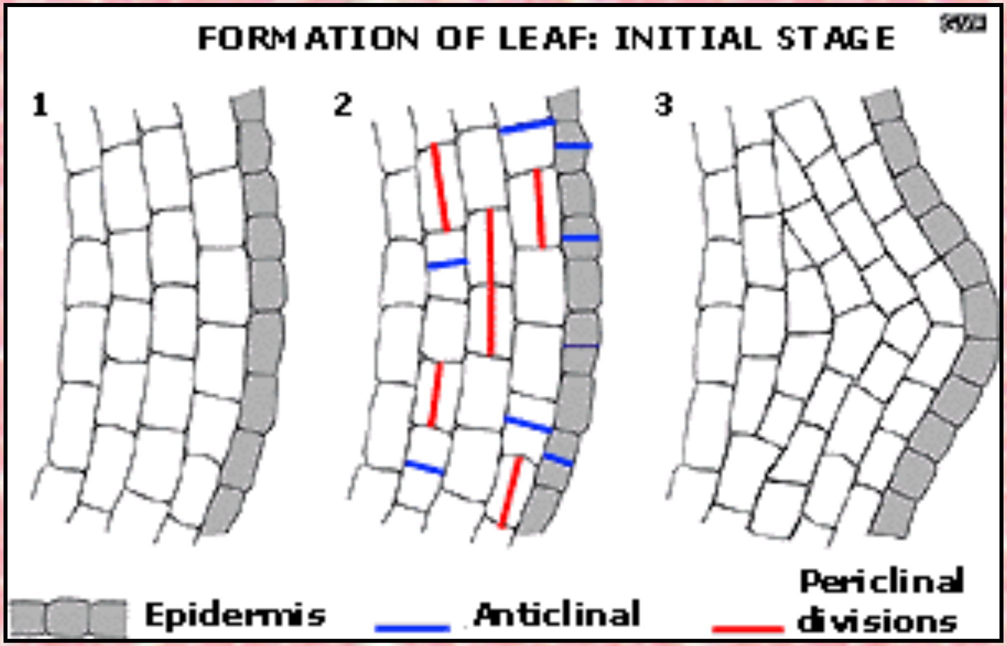
cz: central zone
pz: peripheral zone
rm: rib meristem
sm: shoot meristem

- **During a plastochrone (period of time between the formation of one leaf primordium and the next) the shoot apex change in size**

- **The amount depend on the size of the leaf primordium relative to that of the shoot apex.**

- **Many events occur in the shoot meristem before the appearance of the leaf primordia (we will not go more in these since this is more a "development" process that an "anatomical" one).**

- **The first structural sign that a leaf primordium is developing is the periclinal division of the cells on the apical flank of the shoot.**
- **In dicots it occurs usually in the second and third layer of cell.**
- **In some monocots the periclinal divisions may occur in the surface of the tunica.**
- **REMEMBER: first layer normally originates epidermis! by anticlinal division.**
- **The initial periclinal division is followed by several more resulting in the elevation of the leaf primodium above the surface of the apical meristem.**

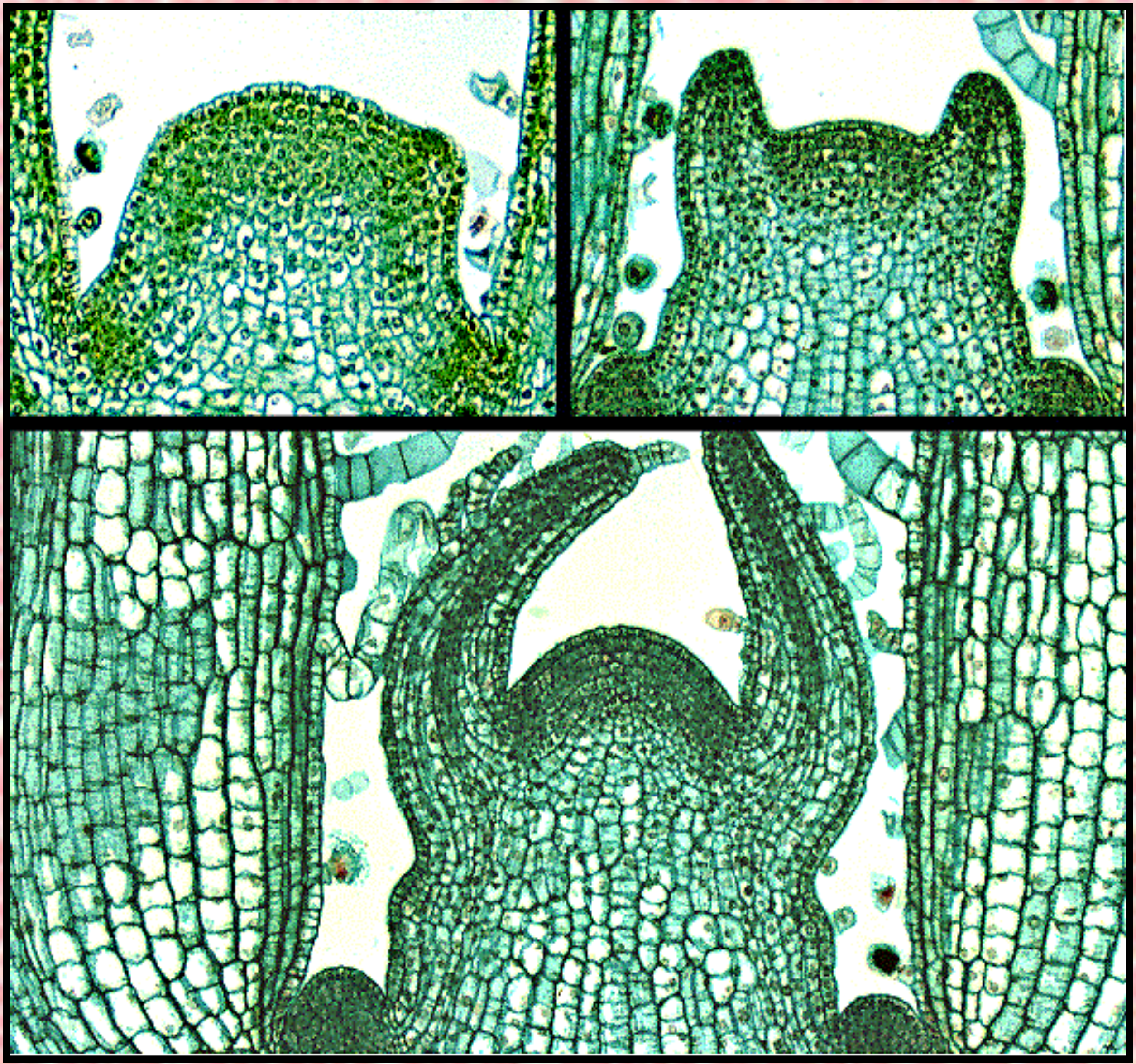


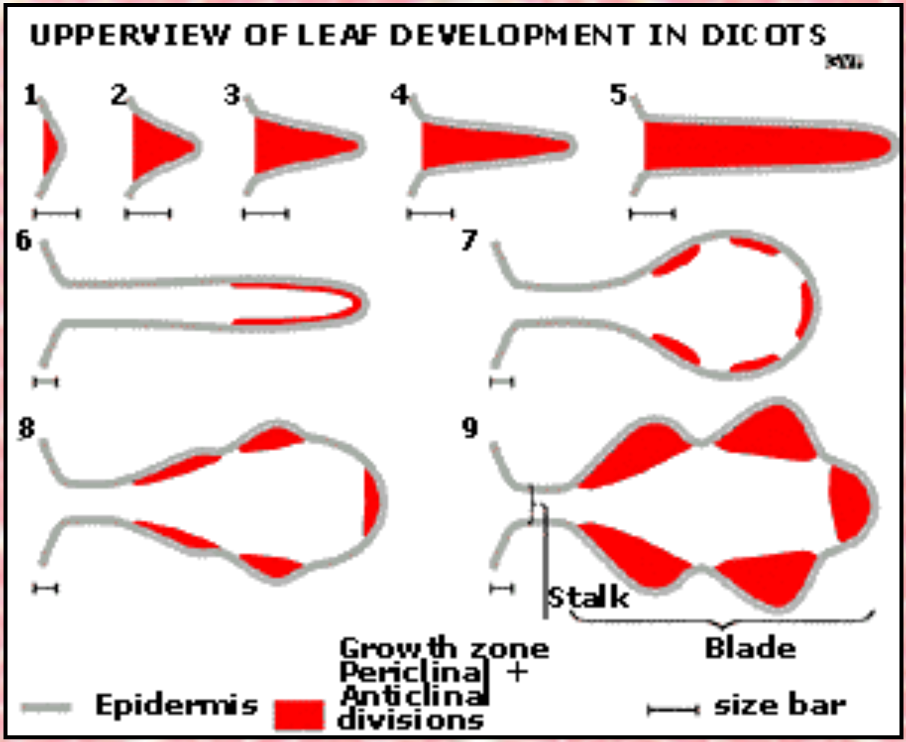
1- Apical meristem

2- Anticlinal divisions (with the division plane at right angles to the surface; the division in parallel to the surface) in the cell layers under the epidermal layer (red in 2). After the first divisions also periclinal (at right angles to the surface) divisions occur the epidermis as well as in the layers underneath (blue in 2).

3- The result is a small bulge (3) that will further develop into a leaf. From this point on, leaf growth differs between monocots and dicots.

Leaf initiation in *Coleus*





1- The initially formed bulge further elongates by mitotic cell divisions throughout the bulge (1-5).

2- Next, at the top of the extended bulge, cells start to divide a single plane causing the bulge to broaden (6).

3- Depending on the species, division activity may decrease or even cease completely (7-9). Thus, the typical irregularly shaped leaf blade of dicots is formed.

4- The lower part of the extended bulge will develop into the leaf stalk or petiole (9).

- **Axillary bud primordia are not formed until the leaf primordium is in its second or third plastochrone**

- **In leaf with stipules, small outgrowth are formed on either side of the primordium base.**

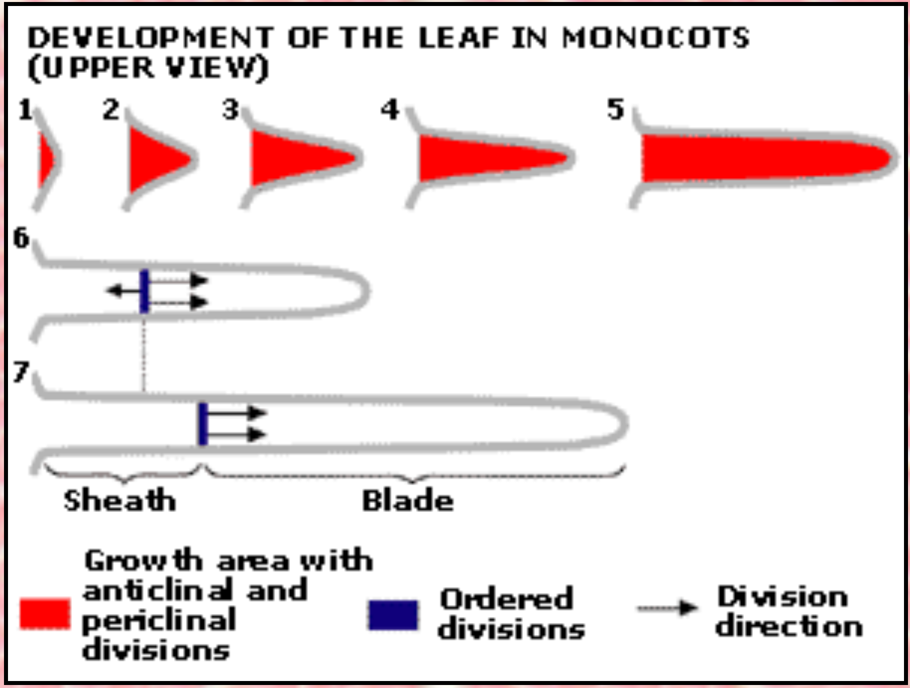
- **Palmately compound leaves the leaflet primordia also become evident on the third or fourth plastochrone**

- **In pinnate leaves the pinnae develop from regions of the marginal meristem and their inception is usually delayed until a later plastochrone.**

What happens with grasses?

- In species with sheathing leaves the divisions spread laterally from the original localized site on the apical meristem ➔ crescent-shaped leaf primordium without dorsiventral symmetry development.

- The primordium growth vertically and the division also spread further around the apex.



1- The initial bulge further elongates by mitotic cell divisions until a certain size is reached. Then growth stops (1-5).

2- Only cells in a small zone at the base of the leaf further divide (6), i.e. nearly exclusively in parallel to the leaf base. This is how the typical long arrays of cells and the parallel venation of monocot leaves arise.

3- Below the division zone a sheath may be formed that surrounds the stem. The top of the extended bulge develops into the leaf blade.

4- Growth may continue without limitation as long as the "intercalary meristem" exists (7). As a result, grasses can resume growth after mowing or grazing.

Apical & intercalary growth

- In early stages after the initiation, around the second plastochrone, the primordium manifests "apical growth".
- It is noticeable as an elongated structure projecting from the apical meristem.
- In many species, vertical growth is greater on the abaxial side of the primordium➔ young primordia tend to bend towards the apical meristem➔ providing protection

- **Apical growth of the leaves ceases relatively early during the development.**
- **Further expansion of the leaves is due to general division of cells and enlargement throughout the primordium**
- **Cell divisions stops at the tip of the leaf first and last at the base.**
- **Extension of the leaf is due to intercalary growth**
- **In monocots, there is a well-defined "intercalary meristem" at the base of the leaf primordium.**
- **Water lilies have a "intercalary meristem" as well (allow the petiole to extend and elevate the leaves above the water surface).**

Marginal growth

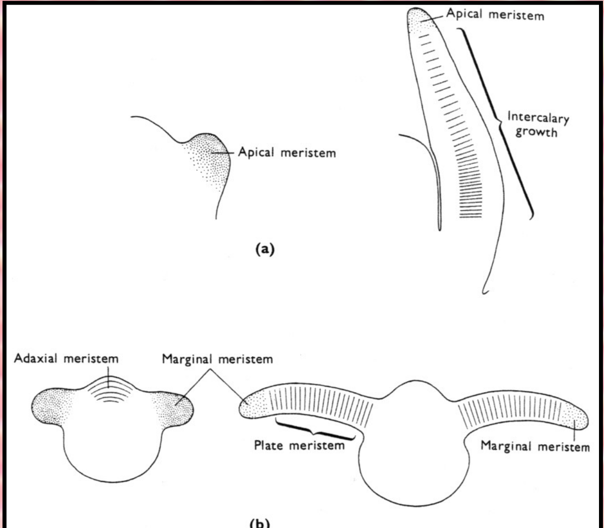
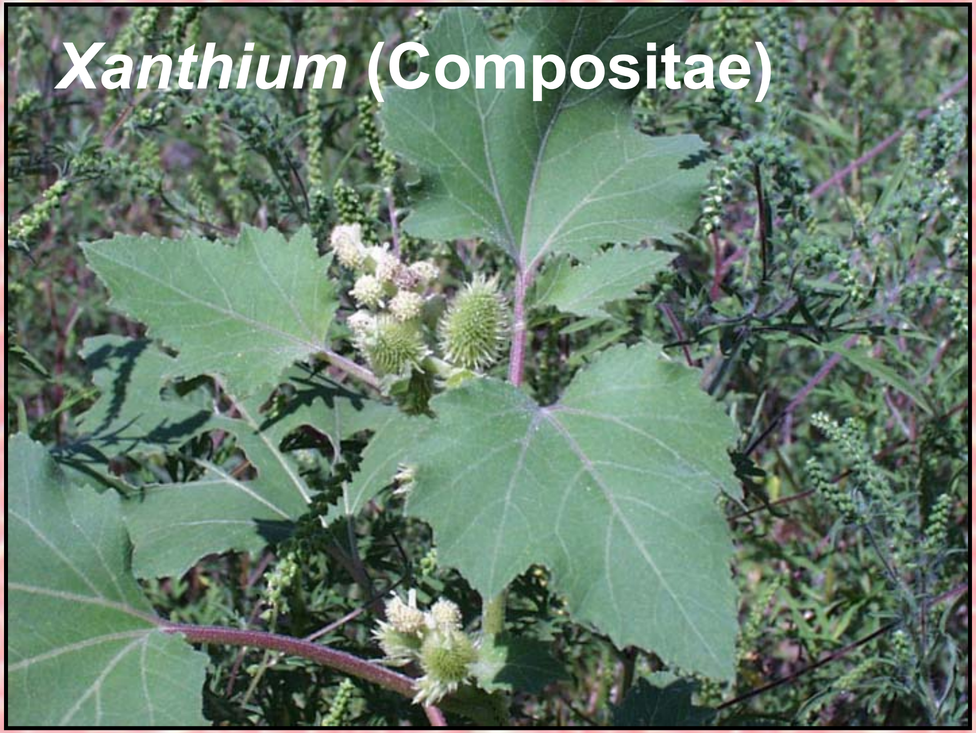


Fig. 5.2 Diagram illustrating the various meristems of a leaf primordium, as seen (a) in longitudinal and (b) in transverse section.

- When the young dorsiventral leaf primordium reaches certain heights, small bulges appear laterally on either side = these are the marginal meristems.
- Marginal meristems will determine the number of layer of the mesophyll cells in the lamina



1- Leaf primordium ~ 0.22 mm at initiation of marginal growth

2- Marginal meristems are active for 23 days

3- 6 layers are established in the leaf

Adaxial growth

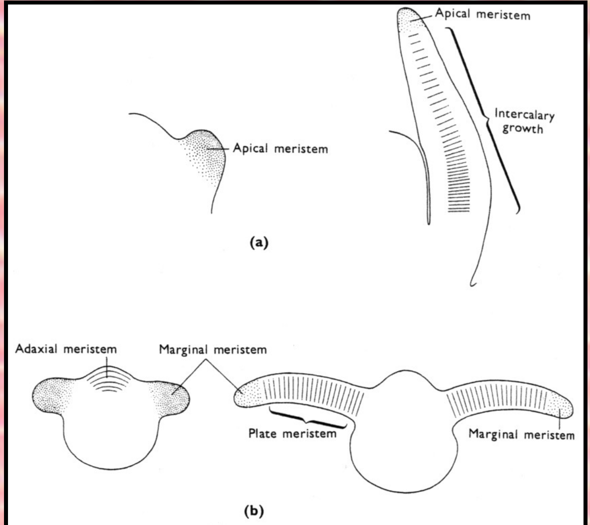


Fig. 5.2 Diagram illustrating the various meristems of a leaf primordium, as seen (a) in longitudinal and (b) in transverse section.

- **In some leaves of dicots a strip of cells below the adaxial epidermis divides periclinally and contributes to the thickness of the leaf = these are called "adaxial meristems"**
- **There are usually located in the center and contributes with the growth of the petiole and midrib (primary vein).**
- **For example in *Acacia* and *Acorus***

Plate meristem

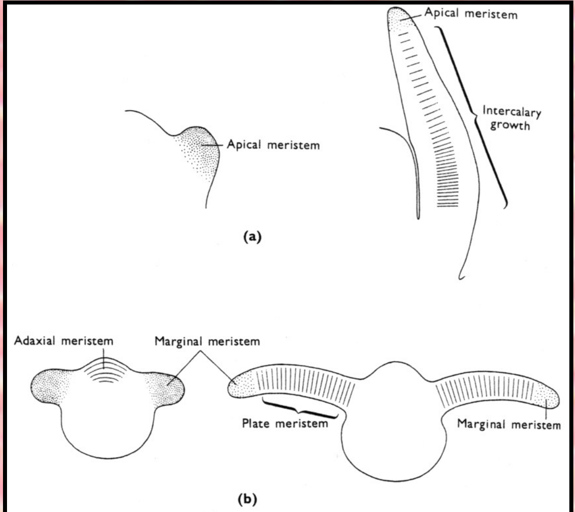


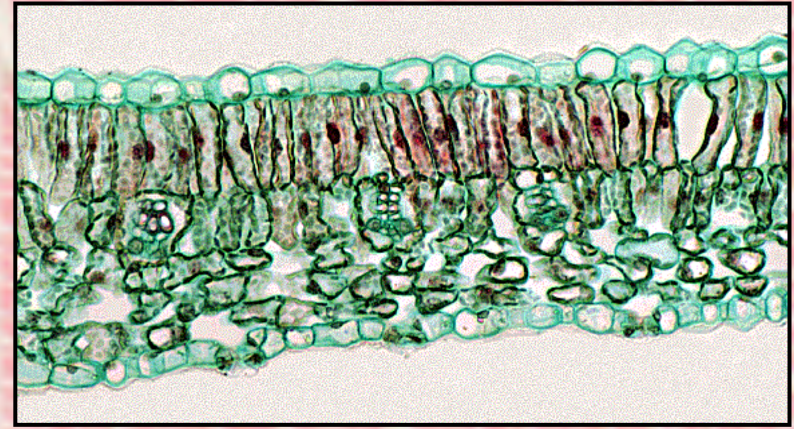
Fig. 5.2 Diagram illustrating the various meristems of a leaf primordium, as seen (a) in longitudinal and (b) in transverse section.

- As result of the activity of the marginal meristems, a certain number of layers of the mesophyll cells become established in the lamina
- These cells tend to divide anticlinally and expand the lamina laterally
- Each cell gives origin to a small “plate” of cells” and the whole lamina functions as a so called “plate meristem”

- **Palisade tissue differentiates from the adaxial layer of mesophyll form by the marginal meristem**

- **Spongy mesophyll from the abaxial layer of the marginal meristem**

SYRINGA (Oleaceae)



- **Palisade tissue differentiates from the adaxial layer of mesophyll form by the marginal meristem**

- **Spongy mesophyll from the abaxial layer of the marginal meristem**

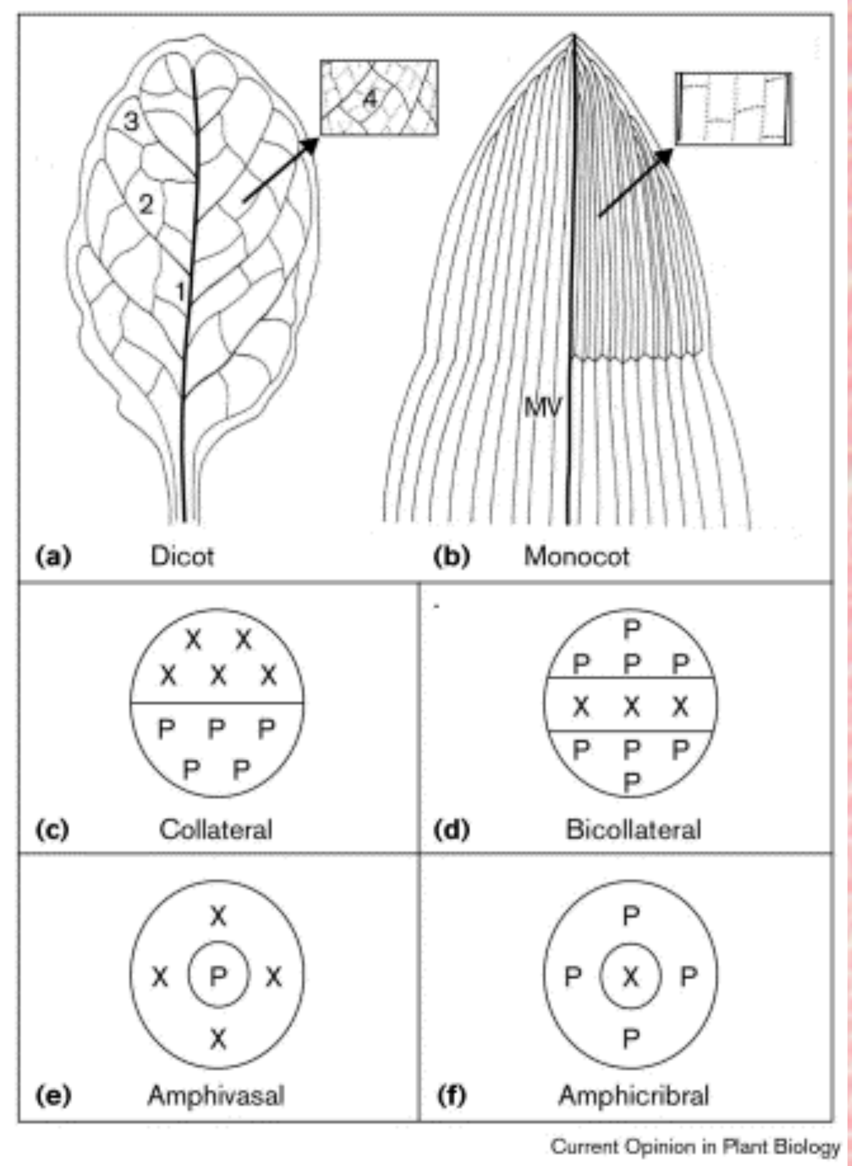
AT THE END…

VENATION PATTERNS

Dicot: initiated by acropetal differentiation of a central provascular strand at the phyllopodium, as the lamina expands more veins are added in a hierarchical model (2^{nd}, 3^{rd}, 4^{th}, etc.). Higher order veins developed from the apical area (basipetally)

Monocot: initiated by acropetal and basipetal differentiation. Higher order veins developed from the apical area (basipetally)

Vascular patterning



(a) In the dicot *Arabidopsis*, at least four size classes of longitudinal veins can be distinguished: (1) primary, (2) secondary, (3) tertiary, and (4) quaternary.

(b) In the monocot maize, a midvein (MV) and at least three size classes of longitudinal veins are present. Small commissural veins interconnect longitudinal veins.

(c–f) Transectional vascular patterns, illustrating variation in the arrangement of xylem (X) and phloem (P) tissues: (c) collateral pattern, (d) bicollateral pattern, (e) amphivasal pattern, and (f) amphicribral pattern.

From Dengler and Kang 2001- Curr. Opin. Plant Biol. 4: 50- 56

SENESCENCE AND ABSCISSION

(PROMISE: this is the last part)

- **Independently of it development and shape, the leaf ultimately undergoes SENESCENCE and ABSCISE➔ falling from the plant.**

- **Deciduous species: every year**
- **Evergreen species: individual leaves abscise after one or more years of growth and development, but all the leaves do NOT fall at the same time.**

- **The activity of the leaves and other determinate organs of the plants is regulated by changes within them and by interaction with other parts of the plant**
- **Leaf senescence is usually characterized by a yellowing of the tissues and by various biochemical changes.**
- **During the whole process different patterns of metabolism may occur.**
- **Structurally, the most important changes occur at the time of abscission**

- **Leaf abscission follows senescence or injury.**

- **Abscission is regulated by several hormones and inhibitors.**

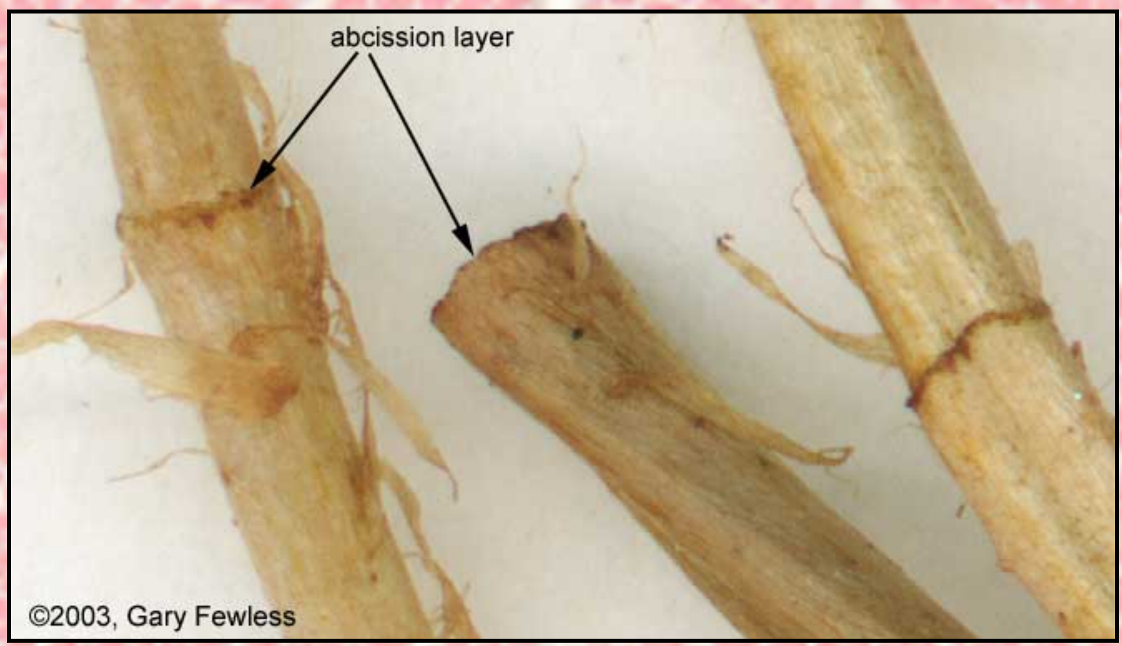
So what is abscission? …

ABSCISSION IS…

Basically, it is a process that involves the separation of the leaf from the stem or basal region of the petiole by separation or lysis of the cells, and the subsequent formation of a suberized protective layer beneath the exposed surface

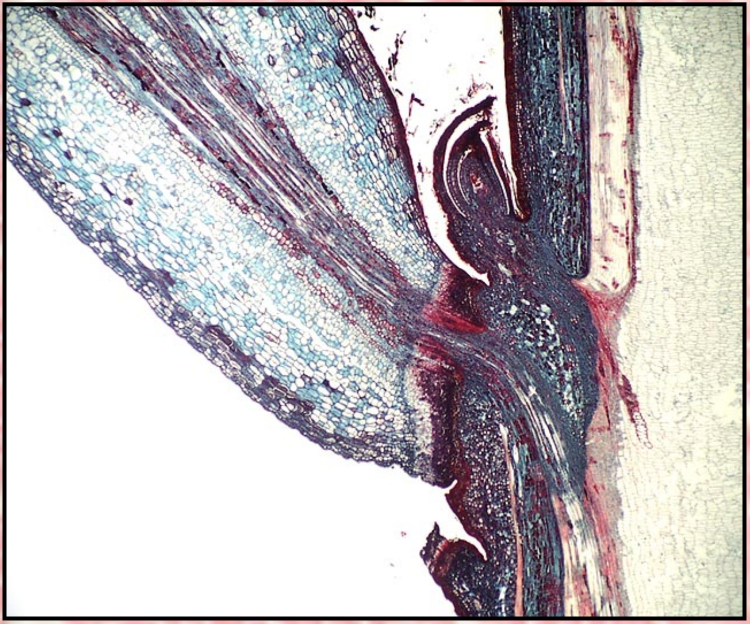
EXTERNALLY

- An abscission zone in present at the base of the petiole
- It is easily recognized by its pale or dark color
- Sometimes it is constricted

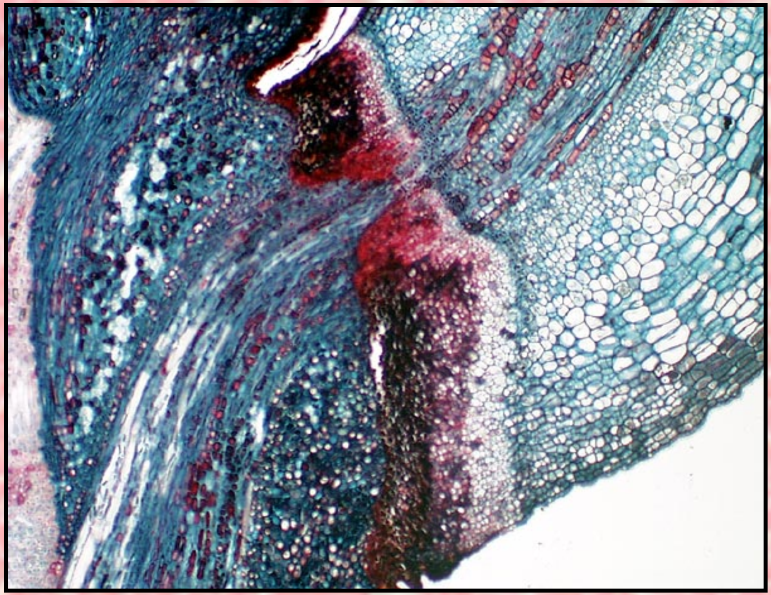


INTERNALLY

- It consists of a region of small, squat cells with few or no intercellular spaces
- Starch is usually absent
- Fibers are very small or completely absent
- It is regarded as a "region of abrupt structural transition" or a "region of weakness"



- The “separation layer” develops in the distal area of the abscission zone
- Starch is accumulated there
- Suberin and lignin may be localized in deep cell layers below the “separation layer”



One example: *Phaseolus*

1- Abscission zone: increase of tyloses in the tracheary elements → may causes water stress

2- Dissolution of callose in the sieve elements→ mobilization of materials to proximal tissues

1 + 2: localized cellular senescence in the abscission zone

SEPARATION

It may occur by:

– Dissolution of middle lamella

– Dissolution of middle lamella and primary wall

– Mechanical breakage involving non-living elements

➔

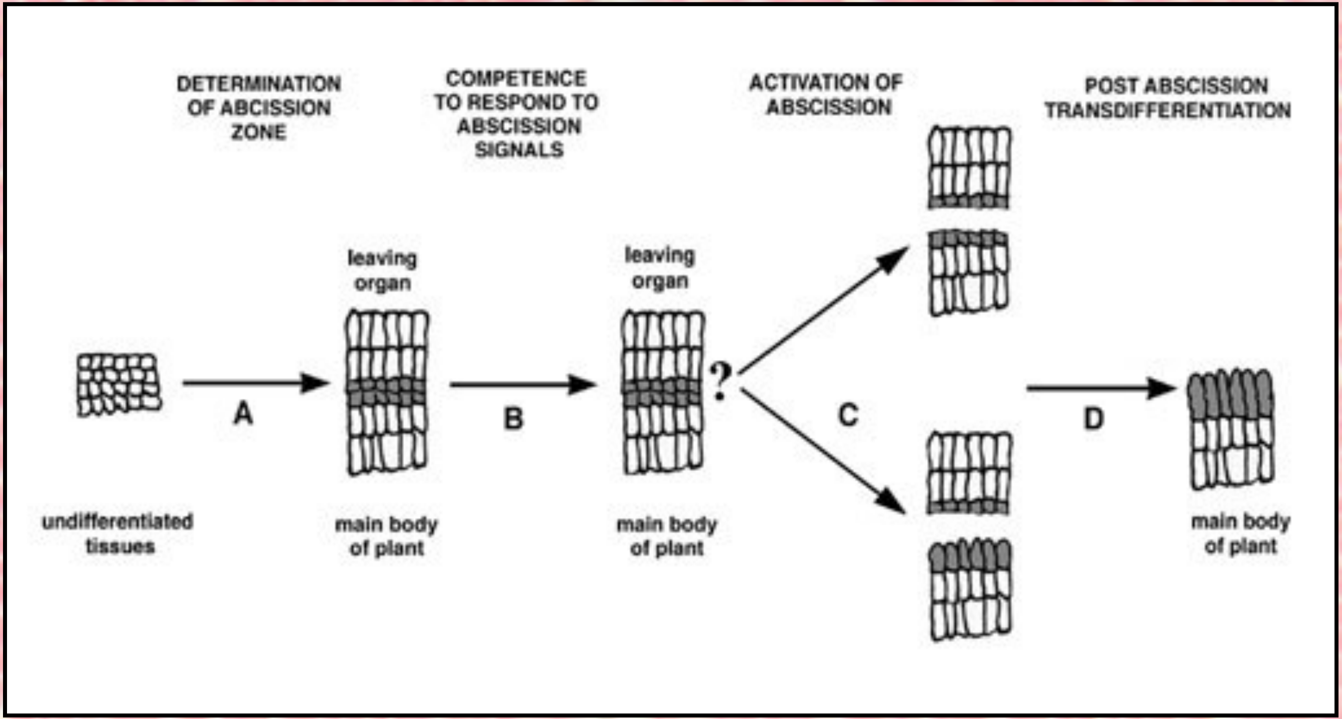
Changes into cell wall and in the enzymes which dissolve pectins, hemicellulose, cellulose, etc.

- **In plants there several hormones that promote and inhibit plant growth**
  - **Growth promoters: *auxins, gibberellins, cytokinins*.**
  - **Growth inhibitors are *ethylene* and *abscisic acid*.**

  - **Hormone levels depend on the day length (photoperiod) along with the temperatures**
    - **Spring's lengthening days and warming temperatures cause trees to produce lots of growth-promoting hormones**
    - **Fall's shortening days and cooling temperatures produce growth-inhibiting hormones.**

- Prior leaf abscission
  - Auxin decrease in the leaf and the abscission zone
  - As leaf become old, there are changes in the efficiency and direction of the auxin transport in the petiole
  - Now, the ABA (abscisic acid) and ethylene becomes involve→ accelerating the abscission time

Abscission process…new version based on *Arabidopsis*



A- Recognition of an ontogeny of the abscission
B- Competence to respond to abscission signals
C- Activation of the abscission process
D- Recognize the trans-differentiation of a protective layer as the last basic step in the abscission-signaling pathway.