# EVOLUTION

## Self study: The Fossil Record

Proterozoic period (630 mln. years ago) —> first algae

Ordovician period (488-444 mln.) —> land consisted of bare rock and sand —> only lichens and algae lived there
Late Ordovician period = first multicellular plants (mosses)

Middle Silurian period (420 mln.) = first “real” plants: primitive spore plants
Devonian period (416-359 mln.) = first vascular spore plants
Middle Devonian —> bigger plants —> trees

Carboniferous period (359-229 mln.) = formation of swamps
Spore plants dominated + some ferns and seed plants
—> fallen trees remained underwater —> no decomposition —> covered by sediment —> “coal forests” with plant fossils

Gymnosperms:
Permian period (299-251 mln.) = new groups of seed plants
Triassic period (251-199.6 mln.) = conifers

Angiosperms:
Cretaceous period (145.5-65.5 mln.) = flowering plants, co-evolution insects —> dominant
Early Eocene period (50 mln.) = large grazing animals + drought —> grasses thrive

# Intro & life cycles

*Dr. Janny Peters - 09/09/2024*

www.science.ru.nl/biologycourses
www.vcbio.science.ru.nl/en/

1. Differences between animals & plants

| | Plants | Animals |
|---|---|---|
| Movement | - | + |
| Nutrition | Autotrophs: photosynthesis | Heterotrophs, indirectly or directly dependent on plants for foor |
| Respiration | CO2 —> O2 | O2 —> CO2 |
| Growth | Continuous throughout lifespan, meristematic tissue | Definite growth, not restricted to particular regions |
| Response | No nervous system, sophisticated systems to react to circumstances | Highly developed sensory and nervous system |
| Cell organelles | Chloroplasts, vacuoles, cell wand, plasmodesmata | - |

2. Specific features of plant cells

Basic foundations of all cells:
- Plasma membrane
- Cytosol with sub cellular components
- Chromosomes
- Ribosomes

Differences prokaryotic - eukaryotic cells:
Prokaryotic cells have no membranes around the nucleus and organelles, but eukaryotic cells do

Animal and plant cells are both eukaryote
Unique for plant cells:
- Chloroplast: green organs, pigment chlorophyll, photosynthetic production of sugar —> conversion of light energy to chemical energy
- Cell wall: extracellular, protection/shape/prevents excessive uptake of water, thick, stiff, microfibrils in matrix = steel enforced concrete, primary —> secondary —> middle lamella ‘glued’ together by pectine
- Plasmodesmata: connecting channel between living parts of cells, connecting cytoplasms of adjacent cells —> transport through symplastic route (vs. apopoplastic route) —> plant cells become one living continuum
- Vacuole: elongated growth by water uptake, storage of water, limited movement due to cell wall

3. Appearance of eukaryotes through endosymbiosis

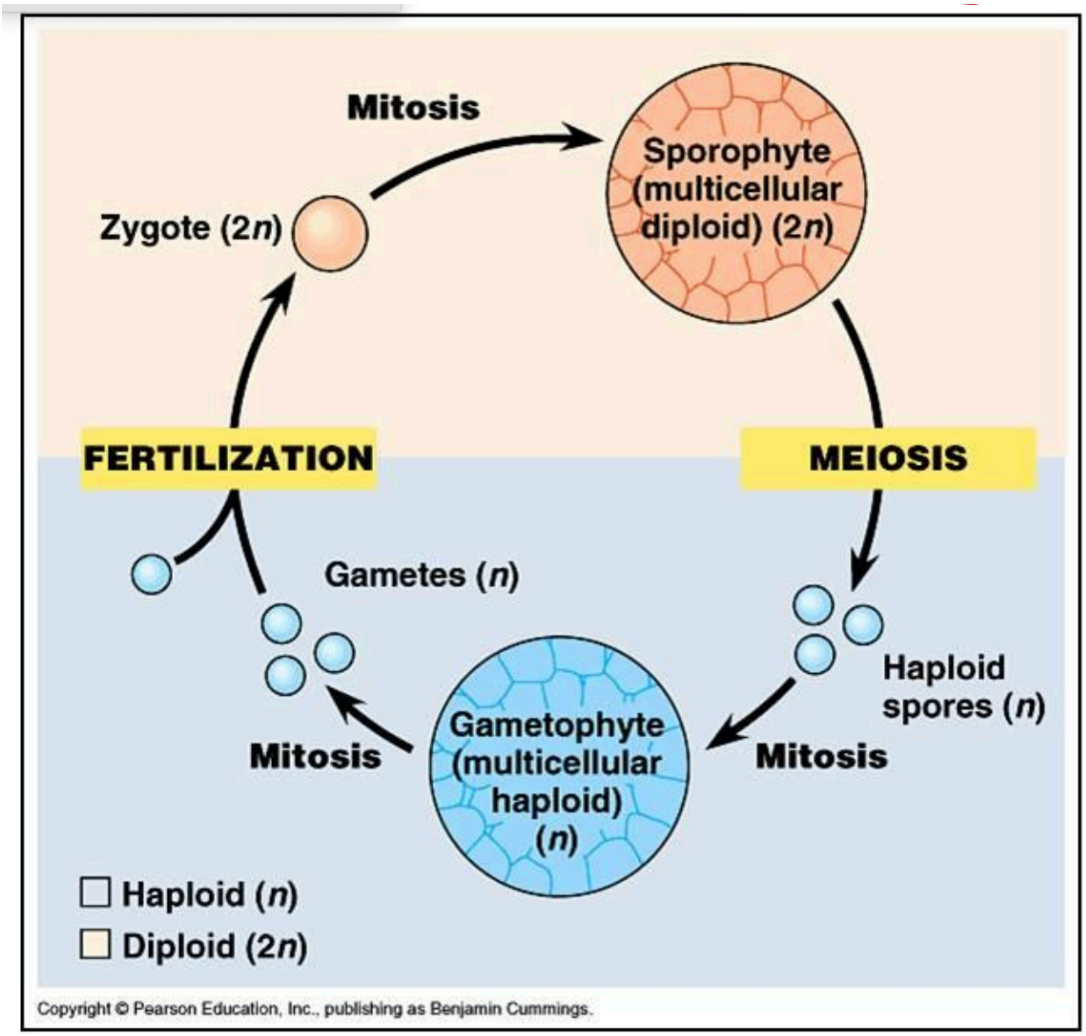
Horizontal gene transfer between prokaryotes (bacteria + archaea) and eukaryotes —> shift from traditional ‘tree of life’ to ‘network of evolution’ = both models are useful

Original chloroplasts and mitochondria were bacteria —> endosymbiosis: pre-eukaryotic host cell + mitochondrion —> Non-photosynthetic eukaryote —> + chloroplast —> photosynthetic eukaryote, etc = serial endosymbiosis hypothesis
Secondary endosymbiosis = the entire (pre-)eukaryote cell itself is engulfed

4. Eukaryotic DNA

Proof for endosymbiosis: Cell organelles that were engulfed through endosymbiosis have… two membranes with unique enzymes and transport systems + replicate by splitting + autonomous: circular DNA (no chromosomes), production of protein + ribosomes more similar to that of bacteria than that of eukaryotes = resemblances of bacteria

5. Plant life cycle




*https://bio11h2015isaiah.weebly.com/alternations-of-generations.html*

| | Diploid stage (2n) | Haploid stage (n) |
|---|---|---|
| **Diplontic (animals)** | Multicellular | Unicellular |
| **Haplodiplontic (plants)** | Multicellular | Multicellular |
| **Haplontic (fungi)** | Unicellular | Multicellular |

Mitosis: 1x 2N —> 2x 2N vs. Meiosis: 1x 2N —> 4x N
Mitosis = growth of cells + multicellular structures from one cell + produces haploid gametes (n) in gametophyte
Meiosis = halving of chromosomes + genetic variability + production of haploid spores (n) in sporophyte

Importance of sporophyte and gametophyte can vary, but cycle is constant

# Algae

*Dr. Janny Peters - 09/09/2024*

Most eukaryotic life forms are small
Green algae are direct ancestors of plants (red and brown algae are not)
All algae are autotrophic through photosynthesis

Primary endosymbiosis —> red + green algae
Secondary endosymbiosis —> brown algae

Algae: holdfast —> stipe —> blade

Brown algae:
- Marine, cool waters
- Heteromorphic = gametophyte (small) and sporophyte (large) have different form

Red algae: LEAST IMPORTANT FOR TEST
- Tropical waters
- No flagellated cells = non-motile —> dependent on currents for dispersion of spores
- Alternation of generations: complex life cycle: 3 multicellular cycle phases to compensate lack of flagella: gametes fuse —> fertilization —> zygote (2n) —> carpogonium (unique for red algae): zygote produce many 2n-carpospores —> develop into many sporophytes —> meiosis to spores (n) —> germinating spores become gametophytes —> cycle (NOT NECESSARY TO KNOW BY HEART)

Green algae:
- Ancestors of plants
- Diverse structure and life history
- Pigment = green = cholorphylls a and b
- Resemble bryophytes and vascular plants, which are adapted to life on land
- Chlamydomonas (moving, unicellular) life cycle: sturdy zygote that does NOT undergo mitosis —> MEIOSIS —> 4 haploid individuals = haplontic life cycle, because zygote (gametophyte stage) is unicellular
- Ulva (sea weed): isomorphic generations = gametophyte and sporophyte have similar form

Charophytes: descendent of green algae, very similar to plants —> beginning stage for plants to acquire traits fit for land life

# Bryophytes

*Dr. Janny Peters - 10/09/2024*

Plants developed from algae —> common traits
- Multicellular, eukaryotic, photosynthetic autotroph
- Cells walls composed of cellulose
- Chloroplasts with pigment chlorophyll a & b
- Flagellated sperm (primitive plants)
- Pigments for uv-protection: beta-carotene and xanthophylls
- Photorespiration enzyme: glycolate oxidase

Shared traits: charophytes + plants:
- Rings of cellulose-synthesizing proteins
- Flagellated sperm
- Eggs encased with protective tissue
- Similar DNA: nuclear, mitochondrial, chloroplast
- Sporopollenin (zygotes / spores)

Chara: haplontic life cycle

Bryophytes = first land plants, non-vascular, usually cool/humid conditions, thallus, no differentiated tissue, sporophyte is dependent on dominant gametophyte, three types: liverworts, mosses, hornworts

Challenges for land survival:
- Gravity —> rhizoids (anchoring, nutrition-uptake)
- Drought + uv-protection —> cuticle (wax-layer) with stomata/pores for transport.
- Resources: mineral nutrients from rock/soil, direct access to air —> rhizoids (anchoring, nutrition-uptake) + no vascular system, but sometimes specialized cells for water/nutrition uptake
- Reproduction: protection/distribution of gametes and offspring —> protective structures

Cuticle: waxy outer layer
- Prevents desiccation, UV-radiation, microbial attack, mechanical damage
- Wax + insoluble lipid polymers
- Prevents gas flow: diffusion allowed on thin parts, spores/stomata for opening and closing

Rhizoids:
- Anchorage of gametophyte to subtract
- Not composed of different tissues (—> unlike roots)
- Usually no specialized conducting cells

Symbiosis between fungi and plants since early-colonization phase:
Mycorrhizae fungi penetrate plant cells —> mycorrhizae exchanges N and P with glucose from the plant —> mutualism

Bryophytes have no vascular system —> no lignified xylem for support and water-mineral transport, no phloem fore sugar transport —> small organisms

Protection of reproductive cells:
- Spores protected by sporopollenin walls
- Gametes inside multicellular gametangia (archegonia ♀, antheridia ♂)
- Embryo inside of protective tissue

Life cycle (Marchantia, liverwort): thalloid liverwort, alternation of heteromorphic generations, sporophyte dependent on and permanently attached to dominant gametophyte, asexual reproduction enabled by gemme formed in gemma cups

Moss life cycle: haploid gametophyte is dominant, alternation of heteromorphic generations

# Seedless vascular plants (ferns)

*Dr. Janny Peters - 10/09/2024*

Lycophytes ('lower' ferns) + monilophytes ('higher' ferns) = seedless vascular plants
Characteristics:
- Flagellated sperm —> requires water for fertilization
- Sporophyte as dominant structure, branched sporophyte with multiple sporangia, not dependent on small gametophyte (unlike mosses)
- Small yet independent, photosynthetic, heart-shaped gametophyte
- Vascular system
- Differentiated tissues/organ systems (true roots, leaves)
- Homospores by default, sometimes heterospores (male and female)

Vascular system: mechanical support + transport
- Enables axially-arranged transport for long-distance —> xylem + phloem
- Lignified tracheids and vessels of xylem —> biomechanics support —> enables heightening

Dichotomous branching (1 —> 2 = telome) of sporophyte —> more ends of branches —> more sporangia —> more spores

Leaves:
- Microphylls: small leaves, supported by one strand of vascular tissue, primitive, lycophytes
  - Development: small outgrowths (nations) —> gradual extension into enation —> microphylls are formed
- Megaphylls: highly branched vascular system, advanced, monilophytes
  - Development: dichotomous branching —> unequal branching aka overtopping —> prominent and weaker branches) —> planation (flattening out) —> webbing of lateral branches to form a leaf surface
- Sporophyll (monilophytes) = specialized leaves —> production of clusters of sporangia (sori, singular = sorus), megasporophylls bear megasporangia, microsporophylls bear microsporangia
- Lycophytes: sporphylls formed on cone-like structures made from microphylls —> cone / strobili, singular = strobilus

Spore production:
- Homosporous:
  Sporangium —> 1 type of spore —> bisexual gametophyte —> eggs + sperm
- Heterosporous:
  Megasporangium —> 1 megaspore —> 1 female gametophyte —> 1 eggs
  Microsporangium—> microspores —> male gametophyte —> sperm

Fern life cycle (by default), haplodiplontic: flagellated sperm fertilizes egg through water —> zygote —> sporophyte —> sporocytes / spore mother cells undergo meiosis —> haploid spores —> sporangia release homospores —> bisexual gametophyte —> antheridia♂+ archegonia ♀

# Gymnosperms

*Dr. Janny Peters - 12/09/2024*

Gymnosperm (naked seed) = vascular plant with unprotected seeds —> sporophyll (spore-containing leaves) arranged in a cone
- 4 types:
  - Cycacophyta: flagellated sperm, male and female individuals, rare nowadays
  - Ginkgophyta: flagellated sperm, male and female individuals, extinct in wild
  - Gnetophyta: non-flagellated sperm, male and female individuals, two leaves, desert habitat
  - Coniferophyta: non-flagellated sperm, bisexual individuals, most common,

| | Flagellated sperm | Habitat | Occurrence |
|---|---|---|---|
| **Cycacophyta** | + | Dinosaur era | Rare |
| **Ginkgophyta** | + | Urban areas | Only domesticated |
| **Gnetophyta** | - | Desert | Common |
| **Coniferophyta** | - | Humid / cold | Common |

Life cycle: haplodiplontic, pollen contain (multicellular but small) gametophytes, dominant sporophyte = entire tree

All seed plants are heterosporous: necessary precondition for evolution of seeds
- ♀ cone: one megaspore per megasporangium —> one megagametophyte
- ♂ cone: one microspore per microsporangium —> microgametophyte

♂

Branch of multiple male cones —> two microsporangia per microsporophyll containing microsporocytes —> meiosis —> tetrad (4x) of microspores —> 2x mitosis per microspore —> 2 body cells + 1 tube cell + 1 generative cell = pollen grain with sperm-gametophyte within —> sperm carried to egg by pollen tube (no water required)

♀

Ovule = integument + megasporangium (2-3 archegonia) + megaspore/megasporocyte
Megasporangium containing megaspore/megasporocyte remains within parent sporophyte, surrounded by integument (= sporophyte tissue)
Megasporophyll / ovulate scale bears ovule —> 1 megasporocyte per megasporangium —> 4 megaspores after meiosis —> 3 megaspores degenerate, 1 remains —> mitosis —> 2-3 archegonia, each containing 1 egg cell

♂ + ♀

Pollination (pollen reaches ovule) —> fertilization (fusion of sperm and egg cell) —> fertilized ovule transforms into seed
Seed =
- Embryo (2n)
- Food supply (n), derived from female gametophyte
- Protective seed coat (2n), derived from integument

Pollination (spring time):
Ovulate scales separate —> pollen grains sticks to pollination drop on scales —> pollen grain contacts megasporangium —> pollination —> cone scales close up —> pollen grain germinates —> development of pollen tube

Development of megagametophyte:

Pollination —> meiosis in megasporangium (1 month) —> 4 megaspores —> 3 diminish, 1 megaspore develops into megagametophyte (1+ year) —> 1000s of nuclei, followed by cell wall formation (13 months after pollination) —> 2-3 archegonia are formed, each containing one egg —> mature female gametophyte

Pollen grain germination:
Pollen tubed digests its way through megasporangium —> generative cell of male gametophyte divides (1 year after pollination) —> 1 sterile cell + 1 sperm cell —> 1 sperm cell divides into 2 sperm cells (no antheridia are formed) —> mature male gametophyte

Fertilization:
Pollen tube reaches egg cell of archegonium (±15 months after pollination) —> one sperm cell unites with nucleus, the other sperm cell disintegrates —> fertilization

Embryo development:
2-3 fertilized eggs develop into embryos —> multiple embryos (polyembryony), but usually only 1 embryo fully develops —> integument develops into seed coat

Seeds contain two different diploid generations:
- Old generation: seed coat (from integumentary) + remnants megasporangium
- New generation: embryo

# Angiosperms

*Dr. Janny Peters - 13/09/2024*

Angiosperms (seed within a vessel): land plants, seeds enclosed in megasporophylls, haplodiplont
- Further reduction ♂ and ♀ gametophytes —> better protection
- Fusion of sporophylls
- Development of flower (derived from cone)
- Double fertilization, endosperm as nourishing tissue
- Fruit development after fertilization

Lineages:
- Basal Angiosperms: near-extinct, spirally-arranged flowers (waterlilies, magnolia)
- Monocots: only one embryonic leaf per seed (corn, palms, etc)
- Eudiocots: two embryonic leaves per seed (majority, trees, etc)

Fusion of sporophylls:
- Megasporangia are located on the edge of the megasporophyll —> fusion of leaf edges —> vessel is formed to enclose a double row of megasporangia (ovules) —> carpels develop into fruit after fertilization
- Leaflike part of structure reduced until only the microsporangia remained —> anther

Flower:
- Four organs:
  - Sepals: small leaves at the base
  - Petals: larger, colorful leaves for attraction
  - (Tepals): leaves when there is no difference yet between sepals and petals
  - Stamen (♂) : anther + filament, derived from microsporophyll
  - Pistil (simple, or compound of multiple fused carpels) / carpel (1 or more) (♀) : stigma + style + ovary, derived from megasporophyll

Cone converted into flower:
- Cone = spirally arranged —> flattened —> flat spirally-shaped flower = basal angiosperms
- Spirals —> separated whirls —> eudicots + monocots
  - Eudicots: usually 5 organs per whirl
  - Monocots: 3 organs (or multiple) per whirl

Double fertilization:
Pollination (pollen grains from anther on the stigma, pollen tube towards megasporophyte) —>
Fertilization: one sperm cell fuses with the egg cell —> zygote (2n) + endosperm (3n)

Life cycle (haplodiplontic)
Extreme reduction of gametophyte, only a few cells
- ♂ Stamen (microsporangium/pollen sac with 4 pollen grains, microsporocytes) —> microspore (generative cell, tube cell, nucleus) —> pollen grain
- ♀ Ovary with 6 microsporangia —> meiosis of megasporocyte —> 4 megaspores —> 3 diminish, 1 remains —> 3x mitosis —> 8 nuclei —> female gametophyte = embryo sac = antipodal cells with polar nuclei, egg
- Pollination —> 2 sperm cells per ovary —> 1 sperm cell fertilizes egg + other sperm fertilizes central cell —> zygote (2n) + endosperm as food supply (3n)

Anther contains 4 microsporangia, surrounded by tapetum
Microsporogenesis:
- Microsporocyte —> meiosis I + meiosis II —> tetrad surrounded by callose —> callose disappears —> 4 microspores —> polarized microspore —> large vegetative cell + small generative cell —> generative cell comes lose, within vegetative cell —> bicellular pollen —> mitosis —> tricellular pollen: vegetative cell with 2 sperm cells within —> mature pollen = male gametophyte

Megasporogenesis:
Base of carpel —> 3 ovaries-containing ovules connected by one style —> megasporangium within ovary —> 1 megasporocyte within megasporangium —> 2x meiosis —> 4 megaspores —> 3 diminish, 1 remains —> 3x mitosis —> embryo sac with 8 nuclei: central cell with polar nuclei + antipodal cells + egg cell + synergies —> polar nuclei in central cell become one nucleus —> mature female gametophyte with 7 nuclei

Pollination = transfer of sperms cells from pollen grain to one of the three ovaries from the stigma through the style by a pollen tube
(Multiple pollen grains and tubes per flower —> 3 ovaries, but many ovaries within)
- Abiotic pollination, wind (20%)
- Biotic pollination by bees (65%) or other animals —> co-evolution between flowers and pollinating animals

After fertilization:
Flower shrivels —> only the ovary remains —> 2 fertilized cells per ovule —> embryo (2n) + endosperm (3n) for food supply —> cotyledon (first leaf) + hypocotyl (first root) and root cap + integument hardens into seed coat —> seed is formed
Ovary expands to make room for enlarged ovule = fruit

Fruit: protects the fruit, which protects the embryo
- Development:
  - Ovary —> fruit that we eat
  - Sepals + petals + stamen + stigma —> dry / shrivel —> fall of as fruit matures
- Types:
  - Simple: single carpel or fused carpel: i.e. pistil consists of one carpel
  - Aggregate: one single flower with multiple carpels, each forming a small fruit (raspberry)
  - Multiple: inflorescence group (tightly clustered flowers) —> ovary walls thicken and fuse —> one large fruit (pineapple)
  - + Accessory: other floral parts contribute to the fruit
    - Apple: simple, surrounded by enlarged receptacle
    - Strawberry: aggregate, enlarged receptacle with small fruits (the ‘seeds’ are NOT seeds)

Caryopsis (grasses, cereals): dry one-seeded fruit in which the ovary wall (pericarp) unites with the seed coat, so the “fruit” part almost disappears

Fruits are dispersed by abiotic factors (wind, etc) or organisms (eaten, sticks to coat, etc) —> co-evolution between fruit and dispersing organisms

# Orchid Flowers & Fruits

*Dr. Barbara Gravendeel - 16/09/2024*

Orchids evolved highly specialized orchid flowers to suit their pollinators.

Great diversity of orchid species: Why?
- Orchid family is very old —> long time to evolve in many species (dinosaur era)
- Many orchid species have unique pollinators —> high reproductive isolation, limited inter-species genetic exchange

How did orchid flowers evolve to suit their pollinators so specifically?

Sepals -> petals -> stamens -> carpels

ABC-model for flowering plants: 3 classes of genes that work closely together to form flower organs:
- A = sepals
- A + B = petals
- B + C = stamens
- C = carpel

Knock-out experiments
- No C: sepals + petals, A takes over from C —> double flower: septal petal petal sepal, but no nectar production for insects
- No B = sepals, carpel —> sepal sepal carpel carpel,
- No A = carpel stamens carpel

| Knock out | Sepal | Petal | Stamen | Carpel | Shape |
|---|---|---|---|---|---|
| **C** | + | + | - | - | p s s p |
| **B** | + | - | - | + | s s c c |
| **A** | - | - | + | + | c s c |

ABC-model does NOT apply to orchids —> exception!

Differentiated leaves
- Large median petal with callus as lip/“landing platform”, small lateral petals
- Small median sepal, long brightly-colored lateral sepals

Perianth Code model:
- Orchids have different copies of ABC-genes —> much more complicated —> balance between SP (small sepals, small petals) and L (enlarged median petals, small petals)
- Balance to L = enlarged petal dominates, small sepals in between
- Balance to SP = small petals, small sepals
- Only applies to orchids, because other flowers don’t have an enlarged median petal / lip that cannot be explained by the ABC-model.

Oncidiinae model:
- Different sizes of sepals, lips and petals
- Conclusions:
  - Median sepal differs from lateral sepals: expression shifts from AP3 to AGL6 copies
  - Lip and callus have petaloid and staminodal origin

Fruit development: fusion of sporangia-containing leaf structures to form carpels
Orchid fruits are simple fruits, that greatly differ in shape/size/location, containing thousands of seeds

Usually seed dispersal by wind (abiotic).
Vanilla = biotic seed dispersal:
- Vanilla odorata: orchid bee scrapes seeds off the fruit —> stores seeds in hollow hind legs —> collect fragrant seeds in bee hive —> communicate through odor (+ antimicrobial qualities of seeds) = mutualistic symbiosis
- Vanilla pompona: fruits do not open at all, nice scent —> unopened fruits are eaten by small animals —> nutrition for animals + seeds are dispersed through defecation = mutualistic symbiosis

3 types of fruit dehiscence, depending on location of dorsal vascular bundles:
- Loculicidal: open up in the middle of the valves (3 openings)
- Septicidal: open up from the boundaries of the valves (3 openings)
- Septifragal: open up from each side of the placental regions (6 openings) —> orchids

Pericarp layers in dry fruit: exocarp (protection) —> mesocarp (vascular bundles, nutrition, transportation) —> endocarp

Orchid dehiscence process: MADS-box A class genes inhibit MADS-box C class genes —> fruit remain close —> expression of MADS-box A class stop in late development —> expression of MADS-box C class genes —> dehiscence

Required exam knowledge:
- ABC-model: explains genetic basis of sepals (A), petals (A+B), stamens (B+C), carpels (C)
- Perianth model: explains genetic basis of median petal (lip) of orchids
- Oncidiinae model: explains genetic basis of further orchid sepal differentiation
- Fruits are formed by carpels, fertilized modified leaves
- Orchid fruits dehisce septifragally
- Orchids fruits dehisce when MADS-box A class genes, which inhibit MADS-box C class genes, are no longer expressed

# DEVELOPMENT

# Embryo development

*Dr. Janny Peters - 17/09/2024*

Zygote (single cell, 2n) —> enlargement, cell divisions (mitosis, differentiation) —> individual plant

Haplontic life cycle: 2 gametes (n) fuse = fertilization —> zygote (2n) —> mitosis —> multicellular sporophyte (2n) —> meiosis —> spores (n) —> mitosis —> multicellular gametophyte (n) —> mitosis —> gametes (n) —>

Megagametogenesis: 4 megaspores —> 1 develops, 3 diminish —>

Microgametogenesis: microspore —> large vacuole on one side —> polarized microspore —> mitosis I —> generative cell within vegetative cell —> bicellular pollen —> mitosis II —> tricellular pollen (2 sperm cells within vegetative cell) —> mature pollen

Angiosperms: two embryo types:
- Eudicot: two cotyledons, pollen with 3 grain openings, flower organs are a multiple of 4 or 5
- Monocot: one cotyledon, small embryo at the apex, does not fill up the whole seed, pollen with 1 grain opening, flower organs are a multiple of 3

Gymnosperms: ≥2 cotyledons

Dicots = all non-monocot angiosperms —> paraphyletic (no common ancestor, different evolutionary branches)
Eudicots = evolutionary branch of dicots, pollen with 3 grain openings
Other evolutionary branches: basal angiosperms, magnoliide

Embryogenesis, eudicot, may differ between species:
Fertilization —> ovule matures into seed (integuments —> seed coat) —> zygote develops to embryonic plant with rudimentary organs —> asymmetrical division of zygote (basal & terminal cell) —>
—> terminal cell —> cell divisions —> spherical proembryo —> heart-shaped embryo —> torpedo-shaped embryo
—> basal cell —> suspensor (connects maternal tissue to baby plant, “umbilical cord”)
SAM (shoot apical meristem) between cotyledons
RAM (root apical meristem) at the end of embryo axis

All embryogenesis has polarity: polarized along two axes: apical-basal axis + radial axis

Apical-basal polarity (early embryogenesis):
Zygote becomes polarized —> 1st asymmetric division —> two-celled proembryo
—> terminal cell —> 2 longitudinal divisions —> 1 transverse division —> 8-celled embryo —> 1st periclinal division (thicker) —> 16-celled embryo, outer layer becomes protoderm (pre-epidermis)
—> first anticlinal division (broader) —> globular embryo
—> basal cell —> suspensor

Differentiation phases: globular —> heart-shape —> torpedo-shape —> mature embryo:
- Heart-shape: formation of organs starts within cotyledon
- Torpedo-shape: elongation of hypocotyl
- Maturing embryo: space within seed coat is filled, derived from integument
- Basal cell / suspensor is still visible, but is diminished

Recognize for exam: protoderm, ground meristem, pro cambium

Monocot embryogenesis: no SAM, endosperm largely remains, embryo is a small part of the seed, nucellus is more important
Nucellus (2n), derived of megasporangium, nutritional source before endosperm develops

# Germination, meristem, tissues & cells

*Dr. Janny Peters - 17/09/2024*

Germination of full-grown embryo (mature seed): dormant until in a suitable environment —> imbibition (uptake of water —> seed expansion —> rupture of seed coat = germination —> enzymes digest endosperm or cotyledons —> nutrients are transferred to embryo —> development of radicle (=embryonic root) —> shoot tip emerges above soil

Resurrection genomics: reviving archeological biological material, i.e. germination of ancient seeds —> research

Types of germination:
- Epigeal (cotyledon = above): hypocotyl (1st root) located between cotyledonary node and radicle, cotyledons emerge above soil through elongation of hypocotyl
- Hypogeal (cotyledon = below): epicotyl (1st leaf) located between cotyledonary node and plumule, cotyledons remains under the soil by elongation of epicotyl

Apical meristems = initial cells and their undifferentiated derivatives, NOT surrounding differentiated cells, meristem ≠ tissue
M
Meristem development:
- SAM (shoot apical meristem): beginning of primary growth = length
  - Consists of cytological zones with different functions:
    - Central zone (CZ): initial cells divide infrequently
    - Peripheral zone (PZ): frequent division of initial cells, on either side of CZ —> leaves
    - Rib zone (RZ): interior to CZ —> central stem-tissue —> pushes SAM upwards
  - Cell layers:
    - L1 & L2 (tunica): anticlinal divisions (broader), L1 —> epidermis
    - L3 (corpus): varying division planes —> increased tissue volume
    - L2 + L3 —> internal tissue
  - Inside —> outside: procambium —> ground meristem —> protoderm
  - Initial cell = non-differentiated, stem cell, unlimited division
  - —> Derivative cells cell —> formed by initials —> divide to form cells for primary meristem
  - —> primary meristem —> develops into differentiated tissue
- RAM (root apical meristem): similar to SAM, but with early-root tissue

| **Primary meristem of SAM** | **Primary meristem of RAM** | **Primary tissue** |
|---|---|---|
| Protoderm | Protoderm | Epidermis |
| Procambium | Procambium | Primary phloem<br>Primary xylem |
| | Root-procambium | Vascular cylinder<br>Pericycle |
| Ground meristem | Ground meristem | Ground tissue:<br>endodermis + cortex |

Primary root:
- Like shoot: division of RAM-produced cells, differentiation, elongation,
- Unlike shoot: lateral outgrowths (root hairs, lateral roots), further away from the root tip
- Constant quiescent center (QC) low rate of cell division, unlimited division
- Developmental zones (no distinct boundaries):
  - Root cap
  - Meristemic zone: contains initials —> root tissue
  - Elongation zone
  - Maturation zone

Plant organs: leaf + stem + root

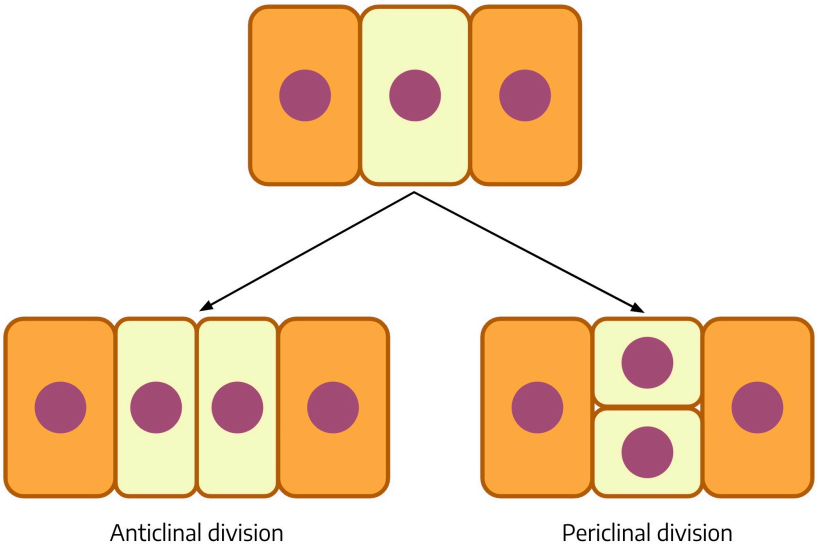
Tissue: dermal + ground + vascular

Cell type:
- Parenchyma: most common (90%), intercellular spaces, diverse functions
- Sclerenchyma: structural support, sclereids and fibers, lignified
- Collenchyma: thickened walls, but flexible, non-lignified

Secondary meristem —> wood (secondary xylem and phloem) + cork

Drawing tissue:
- Single line = wall thickness of parenchyma and phloem cells
- Double line = wall thickness of xylem, collenchyma and sclerenchyma. Distance between lines indicates thickness

Epidermis, derived of protoderm:
- Root epidermis = rhizoderm
- Covered by protective cuticle
- Stomata in leaves and stem
- Sometimes protective hairs
- Root hairs for water uptake



# Root primary growth

*Dr. Janny Peters - 19/09/2024*

Root functions
- Anchorage
- Absorption of water and nutrients
- Storage of food-reserve
- Conduction of metabolic substances and hormones

Two types of root systems:
- Taproot system (eudicot): strongly developed primary root, lateral roots, deep penetration in soil, long-lived
- Fibrous root system (monocot): all roots are equally prominent, short-lived, main root system develops from adventitious roots that originate from the stem, shallow

Symbiosis (95% of plant species) with mychorrizae fungi —> nutrition for mychorrizae + better uptake of nutrients from soil for plants
- Ectomycorrhizae (10%): fungi surrounds outside of the roots, penetrates the apoplast, but not the plant cells itself
- Endomycorrhizae (90%): reach plant cells via apoplast (no penetration: like a finger pricking into a balloon)

Evolutionary adaptions for roots: i.e. roots above-ground/shallow in damp conditions, storage roots for food reserve, etc

Root apical meristem (RAM): endodermis and pericycle unique for roots:
- Protoderm —> epidermis
- Ground meristem —> cortex (parenchym cell storage) + endodermis
- Procambium —> vascular cylinder surrounded by one-celled layer of pericycle

Root growth = continuous process, usually path of least resistance

Root cap = living parenchyma cells = protection of RAM + better penetration in soil + controls growth-direction of roots according to movements/signals from the soil

New root hairs arise just behind the region of elongation, short-lived, constantly renewed, large surface area

Lateral roots arise from the pericycle

Regions (no sharp borders in-between):
Root cap —> region of cell division (RAM) —> region of elongation (few mm) —> region of maturation (differentiation, primary tissue cells mature, production of root hairs, no growth)

Stele (outside —> inside): epidermis —> cortex —> endodermis —> pericycle —> vascular cylinder with xylem and phloem
Eudicot vascular cylinder: tough vascular cambium
Monocot vascular cylinder: no vascular cambium, pith in the center of phloem and xylem

Protoderm —> epidermis (rhizodermis in roots)
- Single layer
- No cuticle
- No chlorophyll
- Large surface area due to root hairs

Ground meristem —> ground tissue
- Cortex with parenchyma cells
- Intercellular spaces (apoplastic transport), plasmodesmata (symplastic transport)

- Endodermis with Casparian strips covered by suberin lamella and lignified cellulose —> water cannot pass through

Transport of water en minerals from root hairs to xylem:
- Apoplastic route: diffusion into cortex via apoplast (intercellular places)
- Symplastic route: through plasma membranes of route hairs —> plasmodesmata
- Transmembrane route: from apoplast to symplast
- Endodermis, controls entry to vascular cylinder: Casparian strip blocks apoplastic passage of water and minerals —> substances can only pass through protoplast of endodermal cells —> filter
- Transport in xylem:

Procambium —> vascular cylinder
- Xylem: water and minerals, star-shaped in eudicots / alternating ring-shaped in monocots
- Phloem: organic substances, alternating ring-shaped in monocots
- Pericycle: 1 cell layer
- Pith (monocots): core of undifferentiated parenchyma cells, surrounded by xylem and phloem

Formation of lateral roots from pericycle, pushes through endodermis + cortex + epidermis by periclinal divisions, each having their own RAM ≠ root hairs

# Root secondary growth

*Dr. Janny Peters - 19/09/2024*

Vascular cambium —> secondary vascular tissues = secondary xylem (wood) + secondary phloem
Pericycle —> cork cambium —> periderm = cork tissue = protective ‘skin’

| Primary meristem | Primary tissue | Secondary meristem | Secondary tissue |
|---|---|---|---|
| **Procambium** | Vascular cambium | Vascular cambium | Secondary xylem<br>Secondary phloem |
| **Procambium** | Vascular cylinder<br>Pericycle | Cork cambium | Cork |

Prevention of rupture: anticlinal division of cambium cell (broader) —> both daughter cells remain within cambium and grow —> increase of circumference/diameter

Activation of cork cambium and vascular cambium —> primary growth stops
Secondary xylem and phloem develop + addition of cork cells —> root thickens

Secondary xylem towards the inside (= wood) > secondary phloem towards the inside

Vascular cambium originates from the space between primary xylem and phloem, and pericycle

Radiating lines / rays of parenchyma cells divide secondary xylem and phloem

Cork emerges from the pericycle to the outer layers —> hydrofobe cork layer—> epidermis, cortex and endodermis dry out and shed + primary phloem is crushed

Eudicot vs. Monocot

| ROOT | Eudicot | Monocot |
|---|---|---|
| **Pericycle** | Gives rise to lateral roots,<br>cork cambium,<br>(part of) vascular cambium | Gives rise to lateral roots |
| **Pith** | - | + |
| **Xylem & phloem** | Limited amount | Numerous |
| **Secondary growth** | + | - |

Epicotyl = shoot tip with a pair of miniature leaves

# Tissue regeneration in plants

*Dr. Victoria Mirnova - 20/09/2024*

Regeneration = replacing or restoring damaged or missing cells, tissues, organs, body parts to (near-)full function

Regeneration methods (seed plants):
- Shoots —> roots
- Stem —> roots + shoots
- Leaf —> shoots + roots
- Somatic cell —> somatic embryo —> plant

Novo organogenesis: grow a whole plant from one leaf

Lateral root formation:
Primary meristem reconstruction:

Plant species differ in regeneration potential.
Research —> increase regeneration potential for agricultural plants

Differences in regeneration potential between different ecotypes (environmentally-distinguished populations) of the same species, dependent on hormonal status:
- Auxin (plant serotonin): distribution of auxin defines efficiency of regeneration
  - Cutting damage —> auxin level rises in basal ends —> inhibits shoot organogenesis
- Cytokinin: cell-division —> promotes plant growth and development

Regeneration efficiency depends on auxin/cytokinin ratio

Consequences of auxin levels, progressive:
- Low: cell growth
- Medium: proliferation
- High: quiescence = optimal

Consequences of cytokinin level, optimum curve:
- Low: differentiation
- Medium: proliferation = optimal
- High: differentiation

Small overlap between auxin quiescence-level and cytokinin (high) differentiation-level = ideal balance —> regeneration

# Stem primary growth

*Dr. Janny Peters - 23/09/2024*

Shoot = stem + leaves
Stem for support and conduction

SAM (shoot apical meristem) is solely responsible for all above-soil primary growth, indeterminate growth
Right conditions —> SAM converted to flower meristem

Shoot structure:
- Nodes with internodes + 1 to 2 leaves per node
- Bud primordia —> apical meristem —> new branches
- Leaf primordial—> apical meristem —> new leaves
- Leaves and axillary buds (lateral shoots, branches) from SAM
- NO pericycle
- NO endodermis
- Pith for dicots (only in stem)

Plumule = epicotyl + long leaves+ apical meristem = embryonic shoot within seed

Evolutionary adaptations of stems:
- Rhizome = horizontal root, occurs in e.g. ferns
- Stolon = horizontally spreading shoots above-soil to spread for reproduction
- Tubers (e.g. potato) = enlarged ends of rhizome or stolon, food storage

Cytological zones of SAM:
- Central zone (CZ), quiescent centre in roots: initial cells, slow division, main production of tissue
- Peripheral zones (PZ): either side of CZ, rapid division, become leaves later on
- Rib zone (RZ): interior to CZ and PZ, central tissue, pushes SAM upward

Clavata-Wuschel feedback signaling coordinates expression of genes for SAM-formation:
- Wuschel amplifies growth, Clavata reduces growth —> delicate balance

Eudicot:
- Bud scales protect apical meristem —> dormancy —> bud scales fall of in spring —> apical meristem is revealed —> primary growth
- Axillary buds develop where a leaf used to be (leaf scar)
- Big bud scars indicate the place where growth stopped last growing-season
- Auxin produced from the top of the stem —> travels downwards through the stem until it encounters an auxin transport inhibitor —> outgrowths

Monocot (e.g. grass, can be mowed and regenerate):
- Apical meristems are close to the soil, not on the tip—> regeneration after being cut
- Extra meristematic tissue (intercalary meristem) in every node to enable length-growth
- Onion is a stem, with meristem at its centre

Structural differences:
- Eudicot: no vascular cylinder, no endodermis, no pericycle (=unlike root), vascular bundles arranged in a ring with cortex on the outside and pith on the inside
  - Order (outside to onside): epidermis —> cortex —> vascular bundles (xylem on inside —> procambium cells in the middle enabling secondary growth—> phloem on outside), pith
- Monocot: vascular bundles scattered in ground tissue, no cortex, no pith, no secondary growth

# Stem secondary growth

*Dr. Janny Peters - 24/09/2024*

Secondary growth —> wood
WARNING: some monocot stems (no sec. growth) resemble wood (palm, bamboo)

Monocot primary growth (palm tree trunk):
- All primary tissue: vascular bundles scattered throughout ground tissue
- No vascular cambium
- Equal in thickness
- No branching

Meristem/tissue development for eudicot stems:

| Prim meristem | Prim tissue | Sec meristem | Sec tissue |
|---|---|---|---|
| Protoderm | Epidermis | | *Shed* |
| Procambium | Primary phloem<br>Primary xylem | Vascular cambium | Secondary phloem<br>Secondary xylem |
| Ground meristem | Pith + cortex | Cork cambium (phellogen) | Cork (phellem) |

Cork originates from the cortex in stems, but from the pericycle in roots.

Periderm = cork cambium + cork —> (a)biotic protection
Epidermis is shed when cork matures
Increased circumference —> empty spaces that develop are filled up with parenchyma

Vascular rays (parenchyma) connect secondary xylem and secondary phloem for interchange of substances

Older cells are further away from cambium cells
- Oldest phloem = most outer ring
- Oldest xylem = most inner ring

Primary growth (from the tip) and secondary growth (further downwards) occur simultaneously.

Xylem:
- Tracheids = long, thin cells with tapered ends, water from cell to cell via pits
- Vessel elements (only angiosperms) = wider, shorter, thinner walled, less tapered, pipe-formation, end walls
- Heartwood = inside, not much transportation
- Sapwood = outer ring, transportation

Phloem:
- Sieve cells (gymnosperms), thin/elongated
- Sieve tube-elements (only angiosperms), wide = alive, no nucleus, no ribosome, no vacuole, no cytoskeleton, have end walls (sieve plates) with pores, companion cell with cell organelles connected to each sieve-tube element via plasmodesmata

Bark = all tissue outside of vascular cambium = sec phloem + cork cambium + cork + periderm

Early (spring) wood: sec xylem with large diameter, thin walls, maximum water delivery to leaves
Late (summer) wood: thick-walled, less water transport, more support, dense
More growth in wet/warm weather than cold/dry weather

Secondary growth —> increased circumference —> epidermis with stomata bursts —> cork becomes external tissue —> parenchyma lenticels from cortex replace stomata —> gas exchange continues

# Leaf

*Dr. Janny Peters - 24/09/2024*

Functions:
- Light interception
  - Conflict: catch light, but no too much uv- and if-radiation
- Gas exchange with atmosphere
  - Conflict: taking up $O_2$ and releasing $CO_2$ without abundant loss of water
- Heat dissipation
- Self-defense from pathogens and herbivores
- Signal perception

Leaf = flattened blade + petiole for connection to the stem
- Simple leaf: 1 petiole, 1 leaf, 1 auxiliary bud
- Compound leaf: 1 petiole, 1 auxiliary bud, multiple leaflets

Eudicot: leaf base extends only partially around the circumference of the node
Monocot: leaf base surrounds the stem

Adaptations:
- Almost always photosynthesis
- Support
- Protection: spinal leaves on cactus stem
- Storage: onion with storage leaves
- Reproductive: plantlets

Early developmental stage:
Peripheral zone of SAM inmates leaf primordial—> orientation of cell division/expansions changes —> 1 young leaves in axil of bud primordial—> differentiation of procambium starting of future central vein = start of vascular development

Initial leaf formation: top meristem —> periclinal divisions (thick/long) —> anticlinal divisions (wide) —>

—> Monocot leaf initiation: most cell division stops —> small amount of cells divide at the leaf base, close to intercalary meristem —> longitudinal arrays of epidermal cells + parallel venation —> continuous leaf growth/regeneration, even when cut

—> Eudicot leaf initiation: different for each species after initial leaf formation —> petiole and branched vein system

Leaf orientation:
- Adaxial side (upside): shiny, large/tubular xylem vessels protrude to upside, some stomata
- Abaxial side (downside): dull, more stomata, phloem extends to underside, lots of stomata

Anatomy:
- Epidermis, covered by cuticle
- Stomata
  - Eudicots: randomly arranged, no subsidiary cells
  - Monocot: parallel arranged, subsidiary cells for opening/closing
- Mesophyll (ground tissue)
  - Palisade: columnar cells, adaxial, intercellular spaces, many chloroplasts —> photosynthesis
  - Spongy: fluffy, irregular/loose parenchyma, intercellular spaces with connection through stomata, some chloroplasts
- Vascular tissue
- Bundle sheath surrounding vascular bundle, develops from ground meristem

Epidermis (from protoderm):
- Varying thickness:

    - One cell-layer: most common
    - Multi-layered: more protection
- Cuticle, limits water loss
- Transparent
- Stomata:
    - Gas exchange: $CO_2$, $O_2$, water vapor
    - Responsible for 95% of water loss
- No chloroplasts (exception: guard cells close to stomata)
- Sometimes protective hairs

Opening/closing stomata:
- $K^+$-transport into guard cells —> influx of water via osmosis —> guard cells swell —> turgid state —> stomata opens
- Guard cells lose water —> guard cells lose turgor —> flaccid state —> guard cells lose turgor —> stomata closes
- Time of day
- Light (blue-light receptor)
- $CO_2$
- Internal clock in guard cels
- Plant growth regulator, abscisic acid (ABA) closes stomata when wilting occurs

Trichomes = uni-/multicellular extensions of epidermis on leaves and stands, protection from biotic and abiotic stresses, reduction of water loss, reflection of excess light
- Mechanical: non-glandular, shapes that hinder movement, e.g. spikes
- Chemical: glandular, secretion of sticky / toxic compounds

Sun leaf: small and thick
Shade leaf: large and thin

Xerophytes: (seasonally) restricted water acces
    - Reduced water loss: sunken stomata, densely covered trichomes, leaf folding
    - Water storage within leaf or stem
Hydrophytes: overly wet habitats
    - Oval/round leaves for buoyancy
    - Thin epidermis, thin cuticle
    - Stomata in upper epidermis only
    - Reduced vascular tissue, especially xylem
    - Multi-layered palisade mesophyll
Mesophytes: favorable conditions, ideal water/dryness balance, no specialized adaptions

# How land plants changed earth's history

*Dr. Caroline Slomp - 26/09/2024*

Source of nutrition —> co-evolution of plants and animals
Impact on climate and environment —> soil formation, cooling effect, habitat
Geological force —> less erosion, meandering rivers, $CO_2$-$O_2$ ratio in atmosphere

Life on earth: origin of solar system/earth (4.6 Ga) —> prokaryotic micro-organisms (3.5-3.8 Ga) —> archaea, oxygen production by cyanobacteria —> unicellular eukaryotes —> multicellular eukaryotes —> aquatic animals —> first land plants (370 million) —> first land animals

Evidence for land plant evolution:
- Fossils
- Chemical signatures: e.g. carbon isotopes
- Phylogeny: genomic research

Cambrian —> Ordovician (470 million) —> Silurian —> Devonian —> Carboniferous (350 million)

Cretaceous (150-50 million) = emergence of angiosperms

Ordovician (470 million):
- Plate tectonics: mostly tropical continents + Gondwana supercontinent on southern hemisphere —> less isolation —> less biodiversity
- Fresh water green algae (Charophyceae) = earliest land pioneer —> fossils + genetic evidence: evolutionary transition from algae to bryophytes (unclear why this transition took 0.5 Ga)

Adaptations for survival on land, needed to develop in aquatic conditions first:
- Desiccation —> cuticle, pores/stomata, pre-vascular water conducting structures
- Gravity
- Nutrition / reproduction without water currents —> spores
- Radiation (uv + if)
- Temperature extremes

Silurian —> first vascular plants (bryophytes)

Early Devonian —> knee-high plants, distinct xylem and phloem, co-evolution with insects
Late Devonian —> first large forests, lycophyte trees with leaflike fronds and roots, carboniferous coal forests + first gymnosperms

Roots and leaves evolved multiple times independently

Slow development from small to large leaves:
$CO_2$-concentration in atmosphere regulate number of stomata:
- High $CO_2$-level —> high temperature —> less stomata, less water loss, less risk of overheating
- Increased global plant biomass —> binding of $CO_2$ through photosynthesis + plant-induced enhancement of rocks with $CO_2$ —> lower $CO_2$-level —> lower temperature —> development of large leaves

Late Carboniferous: large swamp formation among equator (tall trees, ferns, giant insects) —> fossil fuel origin

Cretaceous —> emergency of angiosperms: key role in terrestrial ecosystems + driving factor for human food supply
- Fast growing
- Co-evolution with animal life
- Adapted to warmer regions