Evolution of the Woody Growth Habit -
Land Colonization and Adaptation

- Trees or tree forms plants are classified into
  - Ferns
  - Gymnosperms
  - Angiosperms

- Plants apparently first emerged on land from their forerunner algal ancestors during the mid-Ordovician period, some 460 Mya.

- Remarkable evolution changes: generation of specialized cell types, such as lignified (reinforced) secondary cell walls and vascular tissues; formation of protective wood and bark tissues, and other specialized cell types within; the ability to continuously orient/reorient massive photosynthetic canopies; elaboration of a plethora of often species-specific distinct biochemical pathways leading to, for example, chemical defense systems; evolution of distinct plant pollination/reproductive strategies and adaptations, and a myriad of related regulatory processes at the genomic/proteomic and metabolic levels.

Early phases of Land Colonization-
Turgor-Based Stem Support Systems

- The earliest terrestrial plants had features similar to today’s bryophytes (mosses, liverworts, and hornworts), and were thus nonwoody.

- Small in stature

- Transporting water by hydroid cell types

- Covered by cuticle layers

- Significant changes in initial cell wall properties and assemblies of these early plant forms then followed, including that of secondary wall formation/thickening in the late Silurian period around 415 Mya.

Turgor-based stem support system:
Helical thickenings

Early and late tracheophyte developments that ultimately lead to woody tissue. These progressions also reflect the biophysical/mechanical properties of the polymeric constituents conferred within the tracheophyte cell wall composite(s). *Cooksonia* spp. were among the earliest tracheophytes, whose tracheids had decay-resistant helical secondary cell wall thickenings (red arrow) with anatomical structures that allowed for improved overall water transport.
Early phases of Land Colonization—Turgor-Based Stem Support Systems

- Following *Cooksonia* emergence, however, the early plant tracheophytes subsequently diversified, resulting in numerous independent early lineages, as evidenced by the fossil records of *Rhynia Senicaulis*, and *Gosslingia*.

- Within these plant groups, the tracheid secondary cell walls thus essentially became thicker with control of lateral water movement being improved throughout via defined lateral cell wall pits.

Turgor-based stem support system: *Rhynia* sp.

Self-supporting stem system: *Psilophyton* sp.

Mechanical stem strength of early tracheophytes diversified from a system dependent on turgor pressure as in *Rhynia* to a system complemented by a hypodermal sterome fortified by sclerenchyma cells (s) with thick secondary cell walls as in *Psilophyton*.

75–200 cm in height

Stem cross-section

Early phases of Land Colonization—Turgor-Based Stem Support Systems

- Present-day plants. For example, Douglas fir (*Pseudotsuga menziesii*) has helical-shaped secondary thickenings in its tracheids (ht) partially covering the internal surfaces of its primary cell walls.

- Such modifications, in turn, resulted in changes in plant cell wall biopolymer composition and organization, thereby facilitating their functional properties, for example, in terms of being better able to stand upright and for water conduction, and so forth.

Self-supporting stem support system: *Helical thickenings*

- Presence of phenolic-based components, including the structural cell-wall polymers, lignins, to account for the apparent decay-resistant nature of their secondary wall thickenings.

- However, it is yet unclear as to when lignins proper arose.

- Early tracheid-containing organisms had enhanced resistance to implosion that helped maintain turgor pressure, and a means of improved water delivery.

Extant tracheids, such as in Douglas fir (*P. menziesii*) wood, are variations on the basic theme of a primary wall (pw) (i.e., dark background) with internal helical secondary cell wall thickenings (ht) for structural reinforcement (lighter raised surfaces).
**Stem-Thickening Systems—Further Adaptations**

- To diversify into drier environments and compete for sunlight and gamete dispersal, some plant forms shifted from mainly having a turgor-based stem strength to a more self-supporting system.

- by the mid-Devonian period, around 390 Mya, several independent lineages had begun to achieve ‘self-support’ by development of a hypodermal sterome at the periphery of the stem. This consisted of rows of cells with very thick, decay-resistant, secondary cell walls called sclerenchyma.

- Continued evolution and diversification of secondary cell walls within water-conducting and structurally reinforcing sclerenchyma cells later improved water transport and stem support, respectively.

- Several other stem-thickening strategies subsequently arose, including the development of specialized primary thickening as in the extant tree ferns, numerous monocot angiosperms, and cycads. This was also achieved through independent emergence of unifacial and bifacial secondary growth in several very different taxa.

- Of these adaptations resulting in tree forms, however, only bifacial secondary growth succeeded to the extent of giving rise to the diversity of woody species in existence that we so greatly value today.

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**Primary stem-thickening systems**

Mechanical strength in tree ferns is derived from placement of xylem and sclerenchyma to the stem periphery, and accumulation of leaf bases along the entire stem and root growth (sometimes from the leaf bases) to form a root mass along the lower portion of the stem (b). The cladoxylopsid, *Wattiezia*, preceded both ferns and horsetails and reached at least 8 m in height (c). In extant tree ferns, old leaves abscise (white arrows) leaving behind prominent leaf scars (yellow arrowheads), with the remnant leaf bases contributing to primary thickening. Some present-day tree ferns (d) can reach around 20 m in height (not shown). Tall extant monocots, such as palms, have similar primary thickening systems (e).

Stem thickening by primary tissues evolved independently in several taxa, including some extinct lineages, ferns, and monocot angiosperms. The primary thickening meristem (PTM) is derived from the shoot apical meristem (SAM), where the PTM produces leaves that add to stem thickness (a).
Most prevalent extant stem secondary thickening system: the bifacial cambium

(a) Secondary stem-thickening systems: bifacial cambium

- Xylem & phloem production
- Capacity for stem expansion by generation of new cambial initials

(b) Extinct: Archaeopteris sp.

(c) Extant primitive gymnosperm: Araucaria araucana

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This meristem not only produces secondary phloem and xylem, but also regenerates its own cambial initial cells to allow for stem expansion (a). The earliest tree form considered to have bifacial cambium activity was from the genus Archaeopteris (b). This belonged to the progymnosperms, which in turn gave rise to gymnosperms and later angiosperms. Araucaria araucana (c) is an example of a primitive extant gymnosperm.
Seedling growth occurs through the shoot apical meristem (SAM), giving rise to the shoot system, and the root apical meristem (RAM) leading to the root system. Axillary buds are derived from the SAM (a). The SAM affords all primary tissues, including ground tissue parenchyma, epidermis (from protoderm), primary xylem and phloem, and axillary buds leading to either branches, flowers, or leaves (b). Secondary tissues (cross-section view) of the tree trunk include wood (heartwood (HW) and sapwood (SW)), the ray system, the inner and outer bark, and the vascular cambium that produces both SW and phloem of the inner bark (c). The lower image shows a fresh wood section from lilac (Syringa vulgaris) with HW and SW clearly visible (c).

Bark and outer SW (longitudinal view) (d), with the cork cambium producing the outer bark (layers of periderm).

Cross-section and longitudinal views of knotwood from loblolly pine (Pinus taeda) and shortleaf pine (Pinus echinata), respectively (e).

Common Elements of Xylogenesis in Primary Xylem

Xylogenesis in the Zinnia elegans in vitro tracheary element model system, where mesophyll cells are cultured under conditions that induce them to differentiate into tracheary elements. The steps of differentiation are (1) expansion, (2) secondary cell wall polysaccharide deposition, followed by (3) lignification and programmed cell death (PCD).
Common Elements of Xylogenesis in Secondary Xylem

- For angiosperm vessels and fibers, arising from the vascular cambium.
- For vessels of angiosperms, and to a lesser extent for gymnosperm tracheids, expansion is strongly in the radial direction, followed by secondary cell wall production, lignification, and protoplast lysis.
- For angiosperm fibers, expansion is axial as the cells elongate by intrusive growth, followed by secondary cell wall synthesis, lignification, and protoplast lysis.

Pinus strobus dividing cambial cells

(A) start of cytokinesis in radial view; (B) later stage of cytokinesis with extending cell plate and opposing phragmoplasts in radial view; (C) similar stage of cytokinesis in tangential view; (D) enlarged diagram of telophase and initiation of the phragmoplast; (E) beginning of expansion of the cell plate as the nuclei reform; (F) enlarged view of the expanding cell plate and phragmoplasts. (G–J) High-pressure frozen dividing cambial cells of Pinus contorta; Figs. G, H, and I are equivalent to Figs. D, E, and F, respectively. (G) transmission electron micrographs (TEM) showing the initiation of the phragmoplast between the recently separated chromosomes; (H) light micrograph (LM) showing the formation of the cell plate between the reforming nuclei; (I) light micrograph showing the expansion of the cell plate by advancement of the phragmoplast through the central vacuole; (J) transmission electron micrograph showing the greatly extended cell plate and, within the phragmoplast, the delicate newly formed cell plate. Scale bars = 1 µm for Figs. G and J; Scale bars = 10 µm for Figs. H and I.
Primary and Secondary Metabolism

- **Primary metabolism**
  - The biological reactions are essential to maintain life in living organisms and are known as primary metabolism.
  - Plants convert sunlight energy to chemical energy, such as ATP, NADPH, by the mediation of chlorophyll in chloroplasts and synthesize sugars and starch from CO$_2$ by using ATP and NADPH$^+$. These carbohydrates are stored and used for differentiation and formation of plant tissues.

Primary and Secondary Metabolism

- **Secondary metabolism**
  - The metabolisms which are not directly related to maintaining life are known as secondary metabolisms.
  - The products formed by secondary metabolism are called secondary metabolites.
  - Secondary metabolite play a role in reinforcement of tissue and tree body (e.g. cellulose, lignin, suberin), protection against insects, diseases, and plant regulation (plant hormones).
Primary and Secondary Metabolism

- All organisms need to transform and interconvert a vast number of organic compounds to enable them to live, grow and reproduce.
- All organisms need to provide themselves with energy in the form of ATP, and a supply of building blocks to construct their own tissues.
- An integrated network of enzyme-mediated and carefully regulated chemical reactions is used for this purpose, collectively referred to as intermediary metabolism, and the pathways involved are termed metabolic pathways.

The pathways for generally modifying and synthesizing carbohydrates, proteins, fats, and nucleic acids are found to be essentially the same in all organisms, apart from minor variations.

- These processes demonstrate the fundamental unity of all living matter, and are collectively described as primary metabolism, with the compounds involved in pathways being termed primary metabolites.
Primary Metabolisms

- Degradation of carbohydrates and sugars generally proceeds via the well characterized pathways, known as glycolysis and the kerbs / citric acid / tricarboxylic acid cycle, which release energy from the organic compounds by oxidative reactions.

- Oxidation of fatty acids from fats by the sequence called $\beta$-oxidation also provides energy.

Primary Metabolisms

- Aerobic organisms are able to optimize these processed by adding on a further process, oxidative phosphorylation. This improves the efficiency of oxidation by incorporating a more general process applicable to oxidation of a wide variety of substrates rather than having to provide specific process for each individual substrate.
Primary Metabolisms

- Proteins taken in via the diet provide amino acids, but the proportions of each will almost certainly vary from the organism’s requirements.

- Most organisms can synthesize only a proportion of the amino acids they actually require for protein synthesis. Those structures not synthesized, so-called essential amino acids, must be obtained from external sources.

Secondary Metabolisms

- The compounds which synthesized from the secondary metabolisms are so-called secondary metabolites.

- Secondary metabolites are formed in only specific organisms, or groups of organisms, and are expression of the individuality of species.

- Secondary metabolites are not necessarily produced under all conditions, and in the vast majority of cases the function of these compounds and their benefit to the organism is not yet known.

- It is this area of secondary metabolism that provides most of the pharmacologically active natural products.
Secondary Metabolisms

- To make such compounds as sugars, waxes, lignin starch, pigments, or alkaloids, plants utilize very specific enzymes, each of which catalyzes a specific metabolic reaction.
  - The enzymes are proteins called organic catalysts.
  - These enzymes are coded by specific genes in the plants DNA and are made via processes we call transcription and translation.
  - When there is a series of enzymatically catalyzed reaction in a well-defined sequence of steps, we have what is termed a metabolic pathway.

Primary and Secondary Metabolism

- Primary and secondary metabolites leave a “grey area” at the boundary, so that some groups of natural products could be assigned to either divisions.

- Primary metabolites $\mapsto$ Biochemistry

Secondary metabolites $\mapsto$ Natural products Chemistry
### Cholesterol, Camosterol, Sitosterol, Stigmasterol

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Generalized View of a Plant cell and Its Subcellular Compartments

液泡：植物细胞生长时先行形成一些小液泡，这些小液泡逐渐融合成为大液泡，所以成熟的植物细胞中常可见到大型液泡，或称为「中央液泡」。液泡可贮存物质，如醣类、胺基酸、花青素，也和细胞渗透压维持有关。

粒线体：分成内外两层膜。内膜平行排列上有呼吸酵素，行呼吸作用，製造ATP。粒线体有自己DNA和核糖体。

高基氏体：由许多层扁平囊状膜构成，内含酵素。为分泌物合成与蛋白（构成细胞膜的蛋白和分泌至细胞外的蛋白）加工的场所。两侧的小囊泡为「分泌小泡」，装载要分泌至细胞外的物质。

平滑内质网：无核糖体附著，负责脂质的合成及运输。

颗粒性内质网：附著其上的小颗粒为核糖体，是负责蛋白合成及运输（至高基氏体）
Generalized View of a Plant cell and Its Subcellular Compartments

- Cell wall is the primary site for polymerization of cell wall polysaccharides, lignin, and amorphous silica gel in plants that accumulate this polymer.
- Nucleus is the information center of the cell
  - It is surrounded by a double lipid membrane and contains genetic information (DNA) needed to create proteins within the cell.
  - Cytoplasm is the liquid phase of the cell that contain:
    - Majority of the ribosome involved in protein synthesis.
    - Microtubules and microfilaments that provide a physical skeleton for the cell and also action cellular trafficking of proteins and organelle.
    - All the soluble enzymes of the cell not found within organelles or cellular membranes.

Microfilaments

Microfilaments are fine, thread-like protein fibers, 3-6 nm in diameter. They are composed predominantly of a contractile protein called actin, which is the most abundant cellular protein. Microfilaments' association with the protein myosin is responsible for muscle contraction. Microfilaments can also carry out cellular movements including gliding, contraction, and cytokinesis.

Microtubules

Microtubules are cylindrical tubes, 20-25 nm in diameter. They are composed of subunits of the protein tubulin—these subunits are termed alpha and beta. Microtubules act as a scaffold to determine cell shape, and provide a set of "tracks" for cell organelles and vesicles to move on. Microtubules also form the spindle fibers for separating chromosomes during mitosis. When arranged in geometric patterns inside flagella and cilia, they are used for locomotion.
Biochemical Functions of Organelles in Cytoplasm

- Chloroplasts of a plant cell are organelles bounded by a double lipid membrane which contains the enzymes and pigments that perform photosynthesis.
- Mitochondria are also surrounded by two lipid membranes. These organelles are the location of the TCA cycle, the respiratory chain, and oxidative phosphorylation all of which produce ATP.
Biochemical Functions of Organelles in Cytoplasm

- Endoplasmic reticulum (ER) is a system of membrane-bound tubes and flattened sacs that spread through the cell and work in conjunction with dictyosomes (on Golgi bodies) to produce and secrete various compounds as well as to deliver specific proteins and membrane lipids to their proper locations within the cell.

- Peroxysomes are microbody organelles that have the very important function of housing the formation of toxic peroxides that are necessary for other metabolic mechanisms but would otherwise kill the cell.

- Glyoxysomes are specialized peroxysomes found only in the early stages of plant development. They contain the enzymes necessary for the conversion of stored lipids to carbohydrates in such processed as seed germination where photosynthesis is not yet possible.
Biochemical Functions of Organelles in Cytoplasm

- Vacuoles play a wide variety of roles in cellular metabolic, some “waste bins”, but they also play a very important role as a support structure.

- Cyclosis

  Most of the cell’s content are in a continuous state of motion, called cyclosis, and each molecule within the cell is, at a molecular level, experiencing Browing movement.