Basic Concepts of Biology II: Plant Biology

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Contents

Chapter 1

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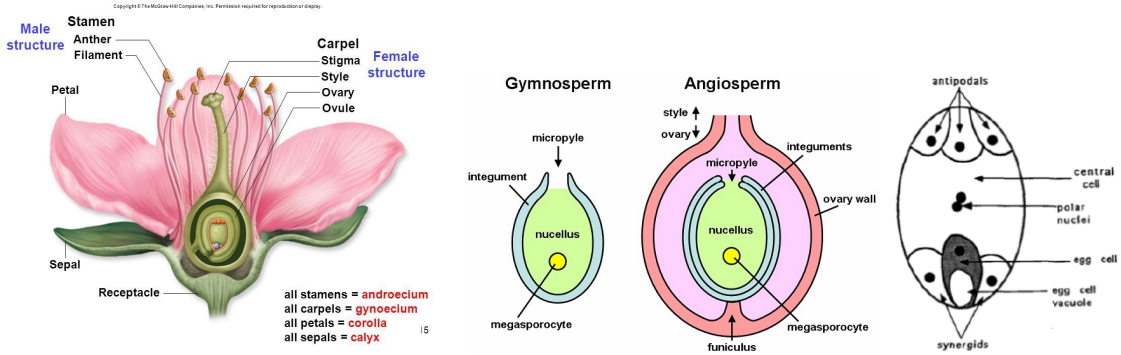
1.1 Reproductive Development

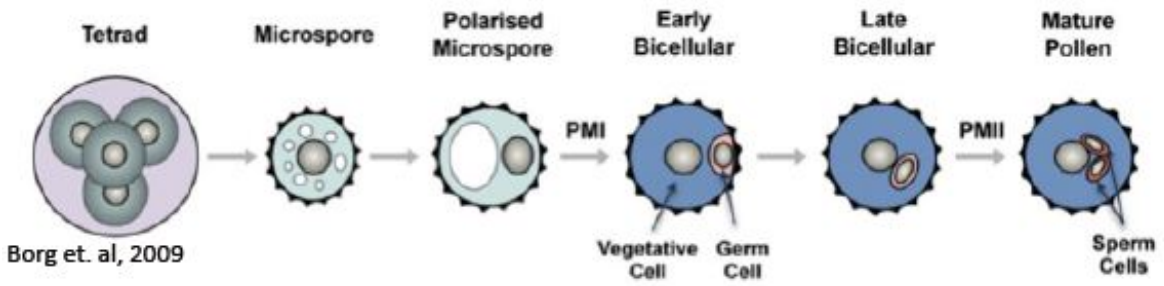
1.1.1 Female Gametophyte Development

The development of the female gametophyte takes place in the ovules of the ovary located in the gynoecium. The ovules contain of a nucellus (megasporangium forming tissue), one or two integuments and a funiculus. The opening of the integuments is called micropyle.
One of the nucellus cells develops into a megaspore mother cell MMC. The process of Megasporogenesis takes place by meiotic cell division of the MMC into four haploid nuclei, from which three degenerate. The remaining megaspore then undergoes Megagametogenesis: Three mitotic divisions result in a multinucleate cell of eight nuclei, which undergo cellularisation (formation of distinct cells). Two of the nuclei fuse to form the nucleus of the central cell.
The embryo sac now contains the following cells: The egg cell (n) located at the micropylar end with asymmetric distribution of cytoplasm, two synergids (n) which interact with the pollen tube during fertilisation, three antipodal cells (n) which have stem cell potential in some plants and a central cell (2n) which is fertilised in the course of triploid endosperm nucleus formation.
The Retinoblastoma-Related RBR Protein in Arabidopsis serves as a tumour suppressor and is required for correct development of the female gametophyte. In mutants, cellularisation does not always take place and the nuclei continue to divide in the absence of fertilisation.



1.1.2 Male Gametophyte development

Development of the male gametophyte takes place within the anther of the stamen. An archesporial cell in the anther divides mitotically resulting in the Pollen Mother Cell PMC and a Tapetal Initial Cell, which develops into the tapetum (nourishing tissue of pollen). The PMC undergoes meiosis, forming a tetrad of four haploid microspores in Microsporogenesis. Enzymes secreted by the tapetal cells lead to the release of the microspores from the tetrad. In the following Microgametogenesis, the microspores enlarge and form a large vacuole. The nucleus migrates to a peripheral position where asymmetric cell division occurs to form one small generative germ cell and one large vegetative cell, which develops into the pollen tube later. The larger cell engulfs the small one, which undergoes one further mitosis and develops into two sperm cells.
The mature pollen grain is surrounded by the pollen coat which contains of a double wall. The internal wall, called the intine, consists of callose and cellulose deposited by the vegetative cell and elongates along with the growing pollen tube during germination. The extine is produced by tapetal cells and contains sporopollenin. The pollen coat develops from the female mother plant (sporophyte).
RBR Protein is required for the correct mitotic division of the germ cell. The vegetative cells divide mitotically instead of the germ cells in mutants and no mature sperms are developed.



1.1.3 Prevention of foreign Pollen Germination and Self-Incompatibility

Pollen from foreign species either fail to germinate or cannot recognise attracting signals from the ovary.
Self-incompatibility is the prevention of self-fertilisation by recognition and growth inhibition of own pollen. It is based on mutual recognition of proteins expressed by the carpel and the pollen, which are encoded in the S-locus. Proteins only interact if they originate from the same allele, which is more likely if carpel and pollen belong to the same individual. Recombination of the S-locus is suppressed during meiosis, such that S-genes are inherited as a single unit. There are two types of self-incompatibility as recognition of the gametophytic (vegetative, germ cells and intine) or the sporophytic (exine) tissue:
Gametophytic self-incompatibility: RNAses of the carpel enter the pollen tube and cut RNA thus preventing growth of the pollen tube. The pollen tube produces F-box proteins which recognise compatible RNAses, marking them for degradation.
Sporophytic self-incompatibility: Recognition is based on the genotype of the pollen parent. The carpel expresses S-receptor kinases which bind pollen extine ligands (cystein-rich proteins, allergens). If the ligand binds, incompatibility is induced via signal transduction.

1.1.4 Pollen tube growth and double-fertilisation

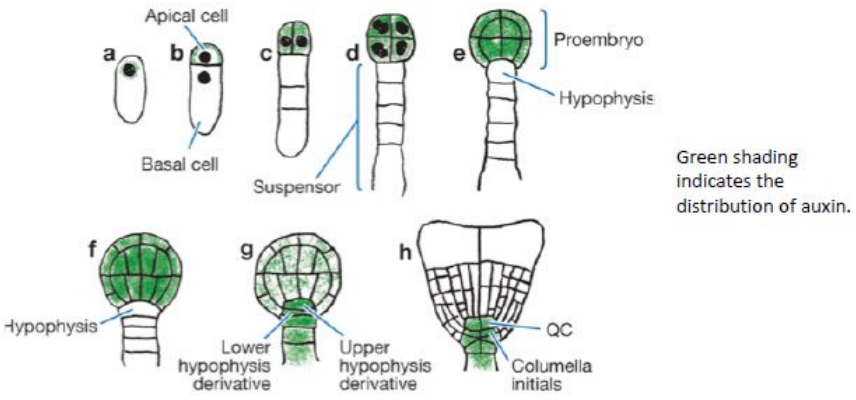
After being deposited on the stigma the pollen tube starts to grow under guidance signals from the carpel and female gametophyte. The pollen tube consists of only one single cell, only growing at the tip and transporting the vegetative and sperm nuclei to the embryo sac. Growth is maintained by calcium gradients: Where the calcium concentration is high, vesicles containing cell wall particles fuse with the plasma membrane. As soon as the pollen tube comes near the entrance (micropyle) to the ovule, micropylar penetration occurs: This process is mediated by LURE peptides, secreted by the synergids, which then bind to the growing pollen tube. The pollen tube necessarily comes in contact with one of the synergids and bursts, such that the 2 sperms enter the synergids. One of them is guided to the egg cell (2n), the other to the central cell (3n). To prevent polyspermy, the ovule dies no longer secrete pollen attracting signals.

1.1.5 Embryogenesis

All angiosperm zygotes develop within a seed. The zygote has asymmetric distribution of cellular components due to the large vacuole which results in asymmetric cell division, leading to a small apical and a large basal daughter cell. The apical cell develops into the embryo and the basal cell into the hypothyse, connecting the embryo to the mother plant, similar to a naval tube. In the apical region the shoot meristem and the cotyledons develop, while the central region forms the hypocotyl and the basal region the root meristem.
Directional auxin transport is required for embryo polarity. In the early embryo, the auxin flow is directed upwards, later it is reversed as it is synthesised at the shoot tip and transported to the roots. The different availabilities of auxin regulate gene expression.

1.1.6 Establishment of Root and Shoot Apical Meristem

The RAM is a population of cells displaying stem cell features at the basal pole of the embryo that give rise to root tissue. The hypophysis cell divides into two daughter cells, from which one divides into four quiescent cells called the quiescent centre QC. The cells surrounding the QC are called functional initials (dt: Initialzellen, pluripotent) which divide frequently and give rise to new root cells. The cells of the QC are called structural initials (totipotent) and divide only to replace functional initials.



The SAM is a group of stem cells at the shoot tip which divide to provide cells for above-ground organs. It is established between the two cotyledons in embryogenesis. Important transcription factors are WUS (WUSCHEL gene), STM (SHOOT MERISTEMLESS gene) and CLV1. STM determines the region of the future meristem and activates meristem-specific genes. STM mutants produce a root meristem instead of a shoot meristem.

1.1.7 Endosperm Development

The triploid endosperm undergoes division without cellularisation resulting in a syncytium surrounding the embryo. As development proceeds cellularisation occurs and the endosperm accumulates nutrients to feed the embryo. The endosperm is surrounded by a layer of living cells the aleurone layer, which produces enzymes required for nutrient mobilisation. In legumes the endosperm is taken up into the cotyledons later on, this is why it is called transient endosperm. In cereals nutrients are mobilised and transported into the embryo (persistent endosperm).
Endosperm development is regulated by MEDEA, which is silenced in male and female gametophytes by methylation. The MEDEA gene is a subunit of the Polycomb Repressive Complex 2 PRC2, which methylates histones. It is only demethylated in the embryo and the central cell where it is expressed upon fertilisation. MEA prevents endosperm development in the absence of fertilisation. This is called parent-of-origin-effect, because it matters which parent expresses which alleles. It does not matter if the male plant expresses MEA or mea (mutant), as it is inactivated by methylation anyway. The plant develops only if the mother plants expresses MEA, otherwise the embryo is aborted.

1.1.8 Seed Development

A mature seed consists of the embryo, the endosperm, the perisperm (nutritive material outside the embryo sac developed by the nucellus) and the testa/seed coat formed from the integuments. Sometimes the seed is surrounded by further maternal tissue as a fruit coat.
After development, seeds usually enter a state of dormancy, where they accumulate storage products and dry out (desiccation). Desiccation allows the maintenance of viability for long periods of time. It is acquired by the accumulation of sugars, synthesis of storage and heat shot proteins and an increase in density.

1.2 Plant Morphology

1.2.1 Cell Wall

Cell Wall Components: The cell wall is a secretory product of the protoplast. It is made up of the following components:

Cellulose microfibrils: 1,4-glucose polymers synthesised by Cellulose Synthase from UDP-Glucose.

Hemicellulose: Various sugar polymers which cross-link cellulose microfibrils.

Pectins: Galacturonic acid, synthesised in the golgi and then transported in vesicles to the plasma membrane via micro tubules where they fuse.

Proteins: Expansins and enzymes like Esterases, Hydrolases and Peroxidases. Synthesised in the ER, transported via MT and fusion with plasma membrane.

Lignin: Phenylpropanoid

Cellulose Synthase Complex: The Cellulose Synthase Complex CSC is incorporated into the plasma membrane where it secretes polymers directly into the cell wall. It consists of six subunits (hexamere made out of CESA proteins) which can synthesise one polymer each. The CSC travels along MT in the plasma membrane such that cellulose microfibrils are distributed evenly. Sucrose Synthase (synthesises UDP-Glucose from UDP-Sucrose) is closely attached by micro tubules.

Cell Wall Synthesis after Cytokinesis: The location of the newly synthesised cell wall is determined by the preprophase band PPB, a ring of MT and actin filaments forming around the cell equator. It disappears during prophase, but leaves an actin-depleted zone. In this zone a phragmoplast (structure of actin and MT filaments between the two daughter nuclei) forms, which guides the formation of the cell plate. Vesicles containing cell wall components move along MT to the phragmoplast and fuse in the actin-depleted zone until the new cell wall is formed.

Plasmodesmata: Primary plasmodesmata form during cell division where the ER crosses the phragmoplast, while secondary plasmodesmata form in non-dividing cells especially after extensive growth. The part of the ER which spans the plasmodesmata is called desmotubule. Plasmodesmata have a defined size which can be adjusted. Normal cargo includes sugars, ions, small RNA and regulatory proteins. Viruses may change plasmodesmata size to ensure their dispersal

1.2.2 Cell Expansion

The vacuole serves turgor regulation, storage of proteins, sugars, ions, bitter compounds, colours and poisons. The vacuole originates from the ER where proton pumps are incorporated. Vesicles from the golgi are taken up into the pre-vacuole. It grows in size or fuses with other vacuoles.

As soluble components inside a cell increase the osmotic potential and turgor pressure rises. To permit water inflow the internal pH is lowered via auxin activated protone pumps resulting in a temporal reduction of hydrogen bonds and activation of hydrolases and expansins. This results in a temporally flexible cell wall which expands due to turgor and osmotic pressure. After cell expansion the stretched and now thinner cell wall is fortified again.
After expansion a secondary cell wall is built, consisting mainly of cellulose microfibrils, hemicellulose and lignin (anti-microbial). This secondary cell wall lies in between the primary cell wall and the plasma membrane. It is important in stability and water-proofing as well as wood formation. The components vary in different cell types as the unique distribution is crucial in differentiation.

The direction of expansion is determined by MT, whose orientation is affected by environmental stimuli and phytohormones. If cellulose microfibrils are unordered, expansion in every direction occurs, ordered cellulose microfibrils lead to directional expansion.

1.2.3 Vascular Tissues

Four vascular stem cells give rise to procambium cells which develop into cambial stem cells and give rise to phloem and xylem tissue, resulting in vascular bundles. Secondary growth of vascular bundles leads to wood formation (lignified dead cells and cellulose).

Xylem: The xylem transports water and minerals and consists of tracheids (dead cells), trachea (in vascular plants, originated from tracheids) and xylary fibers (cells with a thick secondary structure for stability). The formation of tracheids and trachea occurs via programmed cell death: The live cells build up ring-like fortifications in the cell wall and contents of the cytoplasm are degraded step by step and the perforation plates are formed.

Phloem: The phloem transports sugars and RNA. It contains sieve cells, sieve tubes (both live cells without nucleus) and companion cells (metabolically very active). The phloem development is not clear yet, but it includes nuclear degradation and sieve plate formation.

1.3 Shoot Development

1.3.1 Germination

After germination is induced by imbibition, the growing radicle (embryonic root) penetrates the testa (seed coat) and haline and aleurone layers. GA activates receptors on the aleurone layer, leading to transcription of α-amylase genes. The hydrolase α-amylase degrades starch to support the growing seedling. GA is vital vor correct radicle growth and nutrient mobilisation during germination.

Regulation of Dormancy and Germination: Dormancy and germination are controlled by the antagonistic growth regulators abscisic acid ABA and gibberellic acid GA. ABA promotes seed maturation and prevents premature germination, while GA initiates germination. Environmental stimuli as imbibition, while unfavourable conditions induce germination.

1.3.2 Development in light and dark:

Plant growth is regulated in response to light quantity, quality (wavelength) and direction perceived by photoreceptors.

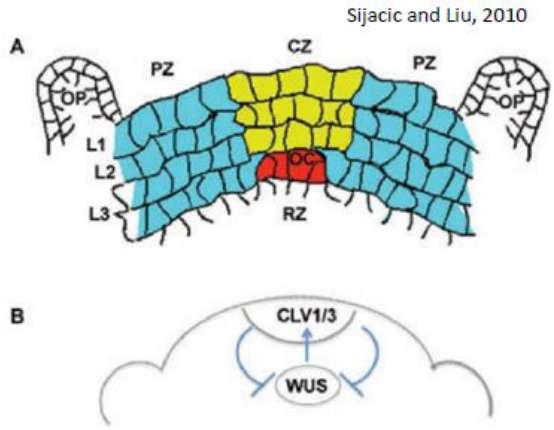
Skotomorphogenesis: Heterotrophic germination and development in the dark, characterised by long pale hypocotyls, no chlorophyl formation and maintenance of the apical hook (protects against underground damage). Underground obstacles induce the production of ethylene leading to shorter and thicker hypocotyls and roots as well as an exaggerated apical hook. This is known as the triple response.
Ethylene is also involved in fruit ripening, seed germination, abscission (dt: Abtrennung),

senescence and response to pathogen attack. It is produced from methionine and inhibits the constitutive inhibition of ethylene receptors thus induces ethylene signalling.

Photomorphogenesis: Autotrophic germination and development in the light. Short hypocotyls, expanded green cotyledons and formation of leaves and internodes. After emerging from the soil, the plant switches to photomorphogenesis in a process called de-etiolation by altered gene expression. In the dark, photomorphogenesis is repressed by COP (DET or FUS) genes. The perception of light via phytochrome (red light) and cryptochrome (blue light) inhibits the effect of previously named genes: Light-activated genes are regulated by the transcription factor HY5. COP1 binds proteins required for photomorphogenesis such as HY5 and marks them for degradation. Cryptochrome, which is also involved in phototropism and circadian regulation, inhibits COP1 vis CRY1 or CRY2 signalling.
The inactive P_r] configuration is activated by red light at 680 nm and switches to the active P_{fr}, which translocates into the nucleus where it interacts with Phytochrome Interacting Factors PIFs. PIFs normally repress photomorphogenesis but are inactivated by P_{fr}.

1.3.3 Development of Shoot Apical Meristem

The SAM maintains the state of the undifferentiated stem cells at its centre and also directs progeny cells towards differentiation such that the total cell number in the meristem remains constant. It generates almost all aboveground parts of the plant and establishes basic geometry. In *Arabidopsis*, the meristem is divided into three layers: L1 (epidermal cells) and L2 (photosynthetic active cells beneath the epidermis) divide anticlinally and form the tunica. The L3 (vascular tissue) cells divide anticlinal (dt: sattelförmig) and periclinal (parallel to the organ surface). The rib meristem at the base of the meristem gives rise to stem cells.
STM and WUS maintain the shoot meristem, while the CLAVATA CLV genes limit its size. CLV1 and CLV2 encode two subunits of a heterodimer and CLV3 the correpsonding ligand. STM activates cytokinin synthesis genes leading to continuous cell division in the meristem. WUS defines the stem cell niche and is expressed in the organising centre OC (red), a stem cell niche below the central zone CZ. In the L1 and L2 layer of the central zone, CLV is expressed where it represses WUS expression. Meaning that excessive WUS activity leads to WUS repression and vice versa. This feedback loop maintains the size of the SAM.



1.3.4 Development of Leaf Primordia

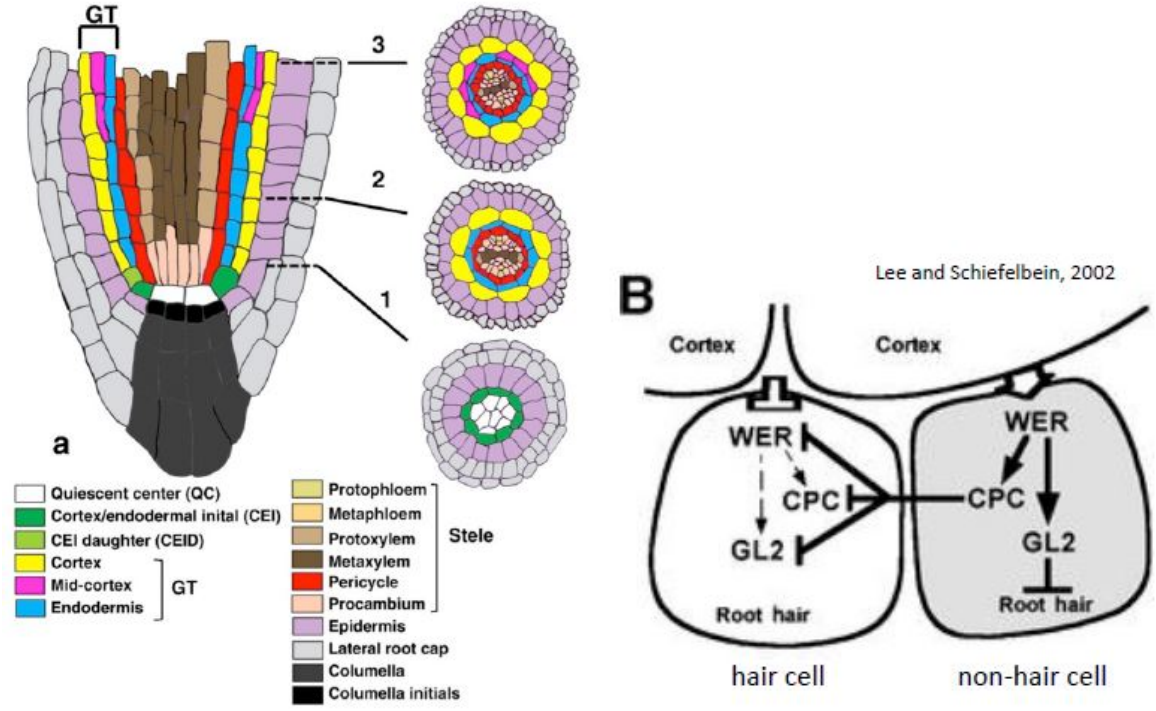
Leves originate as primordia on the flanks of the SAM. A leaf primordia (dt: Blattanlage) consists of one single, two or several leaves on a nod The arrangement of leaves around the stem, called phyllotaxy, is determined by position and timing. Often the primordia are arranged in spirals with an average angle of 137°, because it minimises competition for light among leaves. Existing primordia inhibit the emergence of new primordia in their vicinity, such that new leaves only emerge at positions of least inhibition and maximal auxin levels.

Leaf Polarity: Growth occurs though both cell division and cell expansion. The abaxial-adaxial (thickness) polarity is established by signals originating from the meristem. Cells on the adaxial side (top) face the light and are packed in the palisade mesophyll. Cells on the abaxial side (bottom) are loosely packed in the spongy mesophyll to facilitate the diffusion of gases through stomata.
PHABULOSA PHB and PHAVOLUTA PHV are genes expressed on the adaxial side and confer adaxial identity. The YABBY gene family and FILAMENTOUS FLOWER FIL ensure abaxial identiy.

1.4 Root Development

1.4.1 Development of Root Apical Meristem

The root apical meristem RAM consists of the quiescent centre QC (four niche cells), Cortex/Endodermis Initial cells CEI and other initial cells surrounding the QC. The initial cells divide to form columella cells (vascular tissue), the lateral root cap and epidermis and the ground tissue GT. Cells in the root apex protect the embryonic root during development and degenerate after the root has fully developed. The CEI undergo first anticlinal division to form another CEI and a daughter cell CEID, then they undergo periclinal division to form a cortex and an endodermis cell.
The transcription factors SCARECROW SCR regulates the cell division process of CEI and SHORT ROOT SHR is required fo correct cell division and differentation of CEIs. SHR acts upstream to activate SCR. SCR and SHR are also involved in QC positioning and specification during embryogenesis: High auxin concentration at the basal embryonic end induces expression of PLETHORA PLT genes which activate, together with SCR and SHR, QC-specific promotors. The QC forms where PLT and SCR/SHR expression overlaps.
The QC prevents premature differentiation of surrounding initials by signalling. Differentiating cells signal to the QC to stay undifferentiated in turn. The QC has a more oxidising environment than the rapidly-dividing cells due to Auxin-induced redox changes which slows down the cell cycle.



Root Hair Development: In roots are cells which carry a hair (H cell) and those which do not (NH cells). Whether a root cell is a H or an NH cell is determined by a genetic pathway that inhibits hair cell differentiation. If a cell does not express the inhibitory pathway it develops into an H cell. The expression of this pathway is controlled by three transcription factors WEREWOLF WER, GLABRA2 GL2 and CAPRICE CPC. Overexpression of WER leads to hairy mutants. Only cells which adjoin two cells from the inner cell layer (cortex) develop a hair, while those only verging on one cortex cell do not. Therefore, the determinants of cell fate are most likely located in the cell walls between epidermis and cortex. Upon an unknown signal from the cortex, the NHC expresses WER which in turn activates CPC and GL2. The latter inhibits root hair formation. CPC then diffuses into the adjacent HC where it suppresses WER and GL2 expression.

Lateral Root Formation: The development of lateral roots is induced in the pericycle, where cells upon auxin signalling dedifferentiate and proliferate to build a new meristem under expression of SCR and SHR. This way, a growing lateral root always injures the previously existing tissue. Cell division eventually leads to a new root primordium.

Casparian Strip: To protect the plant from external biotic or abiotic stress without influencing the water and micronutrients uptake the Casparian Strip CS blocks diffusion via the apoplast (cell wall) at the level of the endodermis. The CS is a specialised band of cell wall components and consists of lignin and suberin, making it a water-impermeable barrier. Symplastic transport is still possible via transport proteins incorporated into the plasma membrane. This allows a selective and directional water and nutrient transport.
The CS originates as the Casparian Strip Domain CSD, a plasma membrane domain in the region where the CS later develops. It is characterised by scaffold CASP family proteins

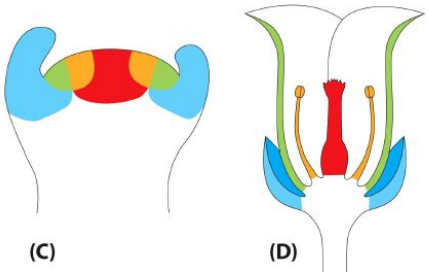
which are involved in correct positioning and building of the CS.
The gene ENHANCED SUBERIN 1 ESB1 is solely expressed in the endodermis and encodes for a guiding protein essential for correct deposition of lignin.

1.5 Flowering

Flowering represents the switch from vegetative to reproductive development. It needs to be controlled precisely to ensure that seed development can be completed. Factors which induce flowering are giberellic acid GA, temperature, vernalisation (cooling of seed during germination in order to accelerate flowering when it is planted) and photoperiod (day length). Day light is sensed by phytochromes and cryptochromes in leaves, which are involved together with negative feedback loops in setting the circadian clock. A long-distance signal moves from the leaves to the shoot apex to induce flowering if the conditions are right.
The gene CONSTANS CO is regulated by the circadian clock and expressed in the leaves. It is stable in the light and unstable in the dark and positively regulates the flowering activator FLOWERING LOCUS T FT gene, which encodes a transcriptional co-regulator SOC1 in leaves. The FT protein enters the phloem and translocates into the SAM where it interacts with the FD transcription factor to activate floral meristem genes such as APETALA1 AP1. Multiple endogenous and environmental factors target the pathway integrators SOC1 and FT, which in turn activate flowering.
A repressor of flowering is the FLOWERING LOCUS C FLC gene which inhibits SOC1 and FT if the conditions are not right. FLC encodes for a MADS-box transcription factor.

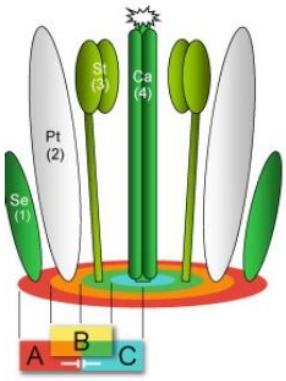
Vernalisation: The plant memorises vernalisation in the SAM over several mitotic divisions. In *Arabidopsis* there are summer and winter annuals: winter annuals flower after cold exposure, while summer annuals flower without cold exposure. Flowering is prevented in winter annuals due to FLC whose concentration is high after long cold exposure.
Vernalisation is an epigenetic response in the shoot apical meristem that involves changes in histone H3 modifications by VERNALIZATION2.

The Inflorescence Meristem: In response to environmental signals the vegetative apical meristem is converted into an inflorescence meristem, which is a transitional stage from vegetative to reproductive growth and may give rise to floral meristems. The floral meristem identity gene LEAFY directs the primordium to develop into a flower meristem. LEAFY is required for specifying floral identity and determinacy thus it is continually expressed under favourable conditions until a threshold is reached that specifies the flower meristem. It activates the transcription factors APETALA1 and CAULIFLOWER.
Unlike the other meristems, the floral meristem produces all flower organs, namely sepals, petals, stamens and carpels. Homo- and heterodimeric complexes of the transcription factors APETALA1 AP1, APETALA3 AP3 and AGAMOUS AG can uniquely specify each organ type. This is explained by the ABC model: A, B and C are the three transcription factors previously named. A and C are antagonists and never form a dimer, while AA, AB, BC and CC do to produce the different flower organs.



(C) Diagram representing the areas of the young floral bud that will give rise to sepals (blue), petals (green), stamens (orange), and carpels (red).

(D) The mature flower.



Chapter 2

Prof. Samuel Zeeman

2.1 Photosynthesis

There is a huge amount of solar radiation striking the earth, thus it is only logical that organisms developed which can live on light about 3.5 billion years. Photosynthesis is the most important process as it results in the assimilation of 15% of the total carbon dioxide in the atmosphere and an energy capture of 100 terawatts. It occurs in the membranes of prokaryotes and eukaryotes. Leafs absorb especially blue, yellow and red light, green is reflected, as well as infra-red and UV light.
Of all the energy hitting a leaf, almost half of it is lost because it lies outside the 400-700 nm active range. 30% is lost due to incomplete absorption and 24% is lost as heat in photochemistry as not all of a photon's energy can be used. From the remaining 28.2% of energy, 68% is used to create sugars of which 40% is respired at night into ATP.

Architecture of Chloroplasts: The outer membrane of chloroplasts is thought to derive from the host cell. The inner membrane is derived from the endosymbiont. The stroma is a highly concentrated enzyme solution (mostly from the calvin cycle). The thylakoids are divided into stromal and granal (stacked) thylakoids, which derive from the inner envelope. Plastoglobules are lipoprotein subcompartments of the chloroplast that are permanently coupled to thylakoid membranes and contain biosynthetic enzymes.
There are different pigments: Chlorophyll a, b and carotenoids, which absorb at different wave lengths. They are held in specific orientations within integral membrane proteins, where they transfer energy by inducing conformational changes. The light-harvesting complex (or antenna complex) is an array of protein and chlorophyll molecules embedded in the thylakoid membrane, which transfer light energy to one chlorophyll a molecule at the reaction centre of a photosystem. The core of the light harvesting complex is predominantly made of chlorophyll a, while on the outside there is mainly b.

Excitation: Light energy induces delocalisation of electrons in pigments which pass their energy by Förster resonance energy transfer from Chlb to Chla and then on to the "special pair" of Chla. This pair does not just pass on the excitation energy but transfers an electron in a process called charge separation. This electron is then transferred to $NADP^+$, where NADPH and ATP are formed in the stroma.

Electron transport chain: PSI can absorb until a higher wave length than PSII but it cannot function on its own, because it is part of the electron transport chain. Manganese delivers the electrons onto the special pair and is oxidised in turn until Mn^{4+} and then splits water to oxygen. Plastoquinone PQ and plastocyanin PC are electron carrier proteins. PSI re-energise the electrons from plastocyanin by passing them onto the iron sulphur clusters and onto ferredoxin. PSI reduces $NADP^+$ to NADPH and the electrochemical proton gradient fuels the ATP synthase.
The photosystems are not uniformly distributed across the thylakoids. In the folded part of the thylakoid membrane, there is more PSII while on the unfolded parts PSI is more abundant. If this separation was not present, there would be a spill over effect (why?) and disadvantage concerning control of NADPH and ATP produced. Diffusion of the complexes and proteins is a limiting factor. If PSII absorbs too much excitation energy, its gets phosphorylated which enables the complex to diffuse to PSI and give away some energy, such that the thylakoids are partially unstacked. The plant can engage in cyclic electron transport such that NADPH is not produced in excess, this is called state transition from linear to cyclic electron flow.

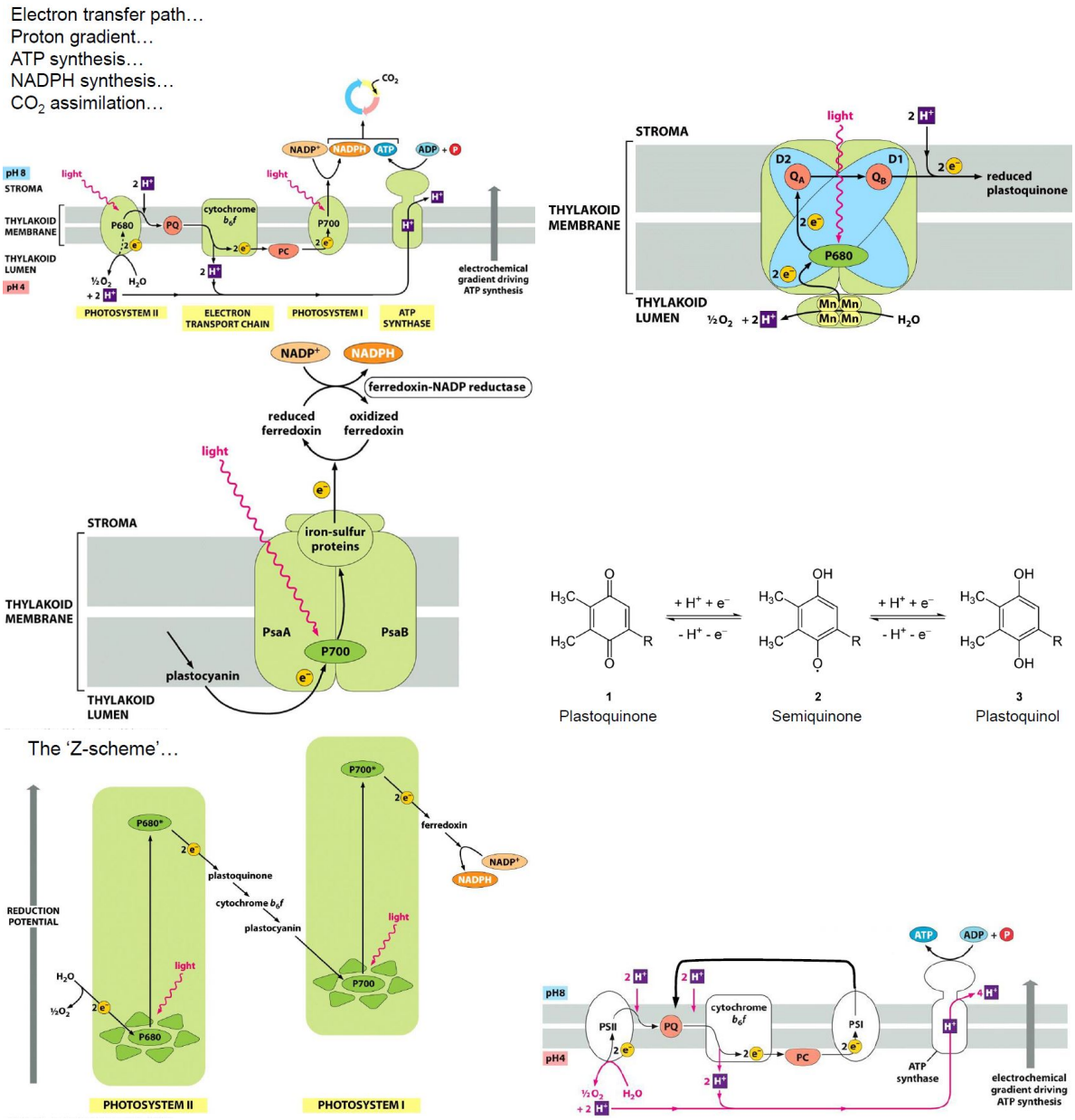


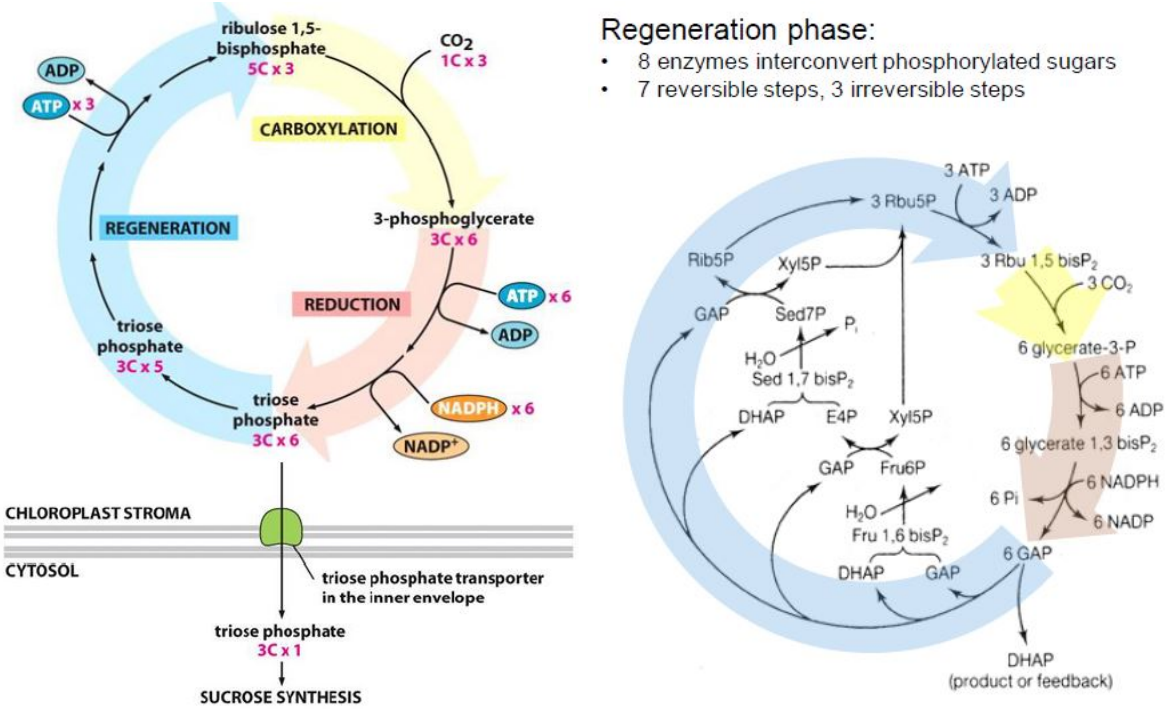
Figure 2.1: a) Electron transport chain, b) PSII, c) PSI, d) Plastoquinone, e) the Z scheme and f) cyclic electron trnasport.

2.2 Carbon fixation

Carbon fixation by photosynthesis can only take place given a certain light intensity (light compensation point), below a particular thresh-hold, plants are loosing CO_2 by respiration.

Calvin cylce The Calvin cycle or reductive pentose phosphate cycle generates reduction potential, ATP and triose phosphate in the cloroplast stroma. Sucrose synthesis takes place in the cytosol.

The Calvin cylce consists of a carboxylation, reduction and a regeneration phase. Carboxylation phase is a single enzyme reaction catalysed by RuBisCO (ribulose 1,5-biphosphate carboxylase/oxygenase) consisting of large and small subunits. In the reduction phase most of the ATP and NADPH generated in the light reaction is consumed. The last part of the cycle is the regeneration phase. Triose phosphate is exported in to the cytosol for sucrose synthesis.



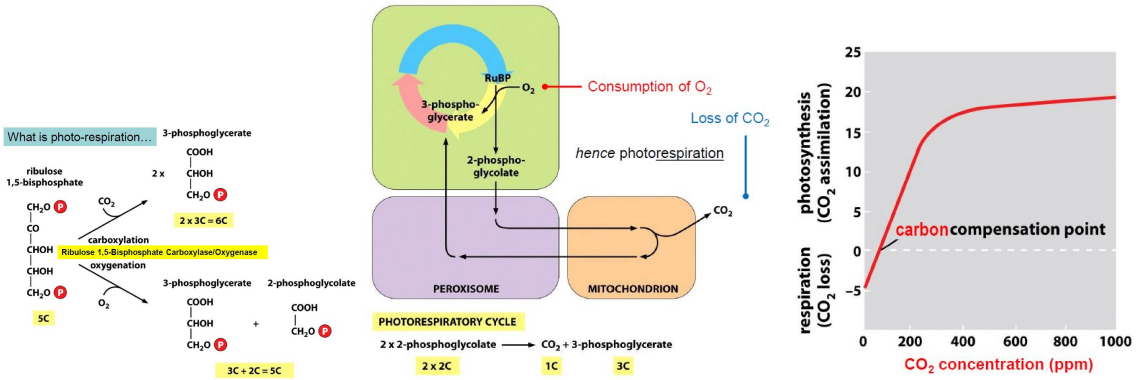
2.2.1 Photorespiration:

RuBisCO is not only a carboxylase, but also functions as an oxygenase in photorespiration. RuBisCO evolved before the oxygen revolution, therefore the activity of the oxygenase did not matter. Today, the oxygenase reaction provides a disadvantage for plants but without the oxygenase domain, RuBisCO's affinity for carbon dioxide would be decreased. It is more selective for carbon dioxide than oxygen however.

The term photorespiration indicates that oxygen is consumed in the calvin cycle and carbon dioxide is produced in the formation of 3-phosphoglycerate out of 2-phosphoglycolate in the mitochondrion. In the phosphorespiratory cycle RuBISCO converts ribulose-1,5-biphosphate to 3-phosphoglycerate and 2-phosphoglycolate under consumption of oxygen, instead of two 3-phosphoglycerate under consumption of carbon dioxide. As 2-phosphoglycolate cannot be metabolised, it needs to be converted back to carbon dioxide and 3-phosphoglycerate, which is an energy loss.

2-Phosphogylcolate is first metabolised to glycolate in the chloroplast, then imported into the peroxisome where it is oxidised to glyoxylate. Via an aminotransferase reaction glycine is generated and taken up into the mitochondrion, where it is decarboxylated and turned into serine under loss of NH_3. The lost NH_3 is used to regenerate the glutamate amino donor. Serine is metabolised to glycerate in the peroxisome which is then turned back into

3-phosphoglycerate in the chloroplast. The carbon compensation point is the threshold where the rate of CO_2 assimilation and loss is balanced. Photorespiration only occurs during stress situations when there is enough light but not enough water, such that the plant cannot grow. It occurs more frequently with higher temperature because the ratio of soluble oxygen and carbon dioxide changes with rising temperature. It is also a mechanism of dissipating excess energy to prevent photo damage.



2.2.2 C_3 and C_4 Photosynthesis

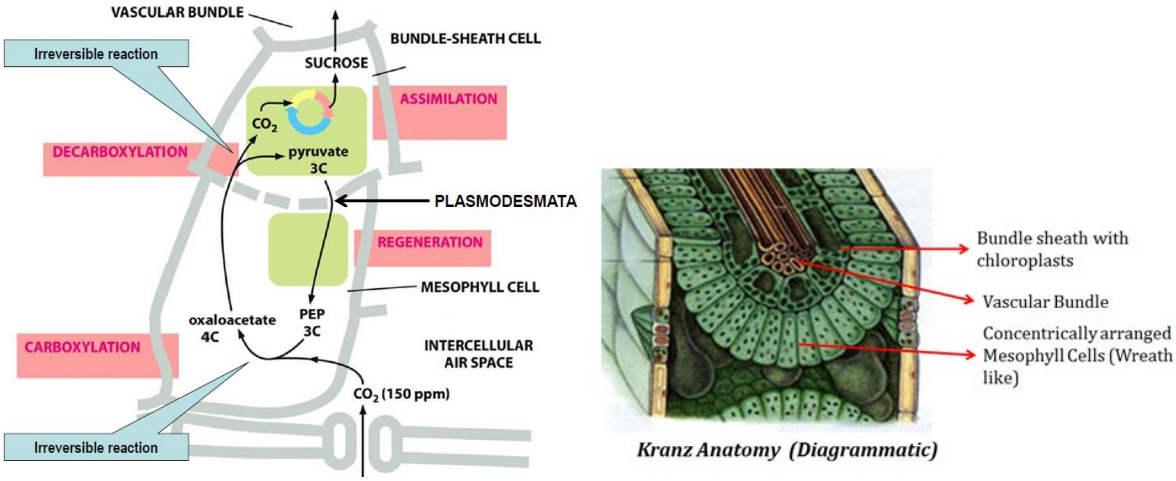
In C_3 photosynthesis the first product of carbon fixation is a C_3 acid, namely 3-phosphoglycerate. Some angiosperms very recently evolved another mechanism; C_4 photosynthesis where the first product of carbon fixation is the C_4 acid oxaloacetate. The light-independent carbon fixation is achieved in a cycle of pyruvate, PEP, oxalacetate and malate. When malate is metabolised to carbon dioxide and pyruvate (irreversible reaction), carbon dioxide is fed into the Calvin Cycle to generate sucrose.

The anatomy of the C_4 plant leaf is adapted to suit this metabolic pathway. In C_4 plants the bundle sheath cells contain chloroplasts and are the site of the Calvin Cycle. Bundle-sheath cells are a layer of cells in plant leaves and stems that forms a sheath surrounding the vascular bundles. The initial fixation of carbon dioxide to form malate takes place in the palisade mesophyll cells, which in C_4 plants form a circle around the bundle sheath. This arrangement, known as Kranz anatomy, ensures that the palisade cells are in close contact with the bundle sheath cells such that the malate can easily pass to the bundle sheath. It also means that the products of photosynthesis can be quickly transferred from the bundle sheath to the adjacent phloem tissue for transport to other parts of the plant.

The main advantage is the reduction of photorespiration: C_4 metabolism is the spatial separation of Carbon-fixation (Calvin Cycle in the bundle-sheath cells) and Carbon-assimilation (C_4 pathway in the mesophyll cells). Bundle-sheath chloroplasts have little or no PS II, meaning they have little or no O_2 production. The electrons flow cyclical through PS I and cytochrome b_6f, leading to insufficient NADPH production. This is compensated by the oxidation of malate to pyruvate where NADPH is produced. Without O_2 no photorespiration can take place, therefore photorespiration is greatly reduced in C_4 plants.

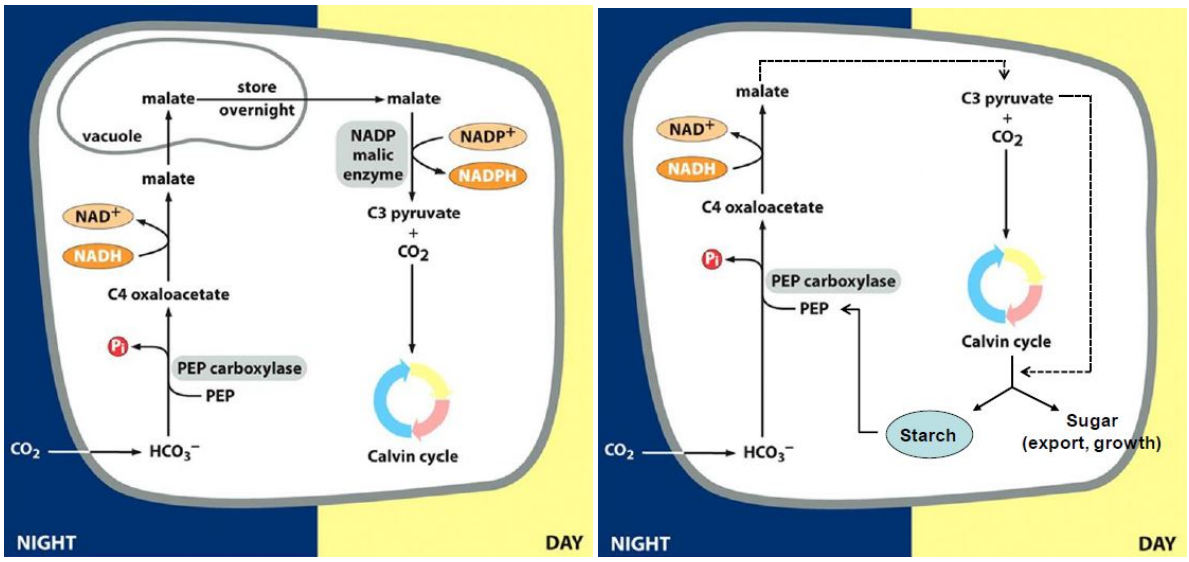
Additional advantages of this supplementary pathway are: The C_4 pathway allows photosynthesis to occur at very low concentrations of carbon dioxide as PEP carboxylase has an extremely high affinity for carbon dioxide. This pathway also works well at high temperatures and light intensity, enabling efficient photosynthesis in tropical plants. In addition, the malate formed can be stored before being used, to be later broken down to carbon dioxide

when required in the Calvin Cycle. This is important in desert plants, which need to close their stomata during the day to reduce water loss (can close their stomata without falling below the carbon compensation point). It proves a major advantage for tropical plants that have high rates of growth and photosynthesis and are adapted to high temperatures, strong light, low carbon dioxide levels, and low water supply. Because of their higher affinity for carbon dioxide, C4 plants tend to grow more rapidly than C3 plants and produce greater yields.
Different variations of C_4 metabolism exist. It evolved more than sixty times in about 20 different angiosperm families. The driver for evolution of C_4 metabolism may have been water deficit, low atmospheric CO_2 and other combined stresses promoting photorespiration in semi-arrid climate zones. Additionally, some of the worlds most important crops are C_4 plants, like maize, sugarcane and sorghum (dt: Hirse). Some C_4 plants even lack Kranz anatomy, the special structure of leaves in C_4 plants where the tissue equivalent to the spongy mesophyll cells is clustered in a ring around the leaf veins, outside the bundle-sheath cells.



2.2.3 Crassulacean Acid Metabolism CAM

CAM is a further development of the C_4 metabolism as an adaptation to arid conditions. It is a temporal separation of carbon fixation and carbon assimilation. Carbon dioxide capture occurs at night and CO_2 is stored in the form of malate. During the day the carbon dioxide is fed into the Calvin Cycle. As there is no need to capture carbon dioxide during the day, the stomata can be kept shut to prevent water loss.
CAM plants evolved already long ago and as in C_4 metabolism there are different variations. The driver for CAM evolution probably was low daytime CO_2. Some crops are CAM plants. In some species CAM is even inducible or tissue specific.



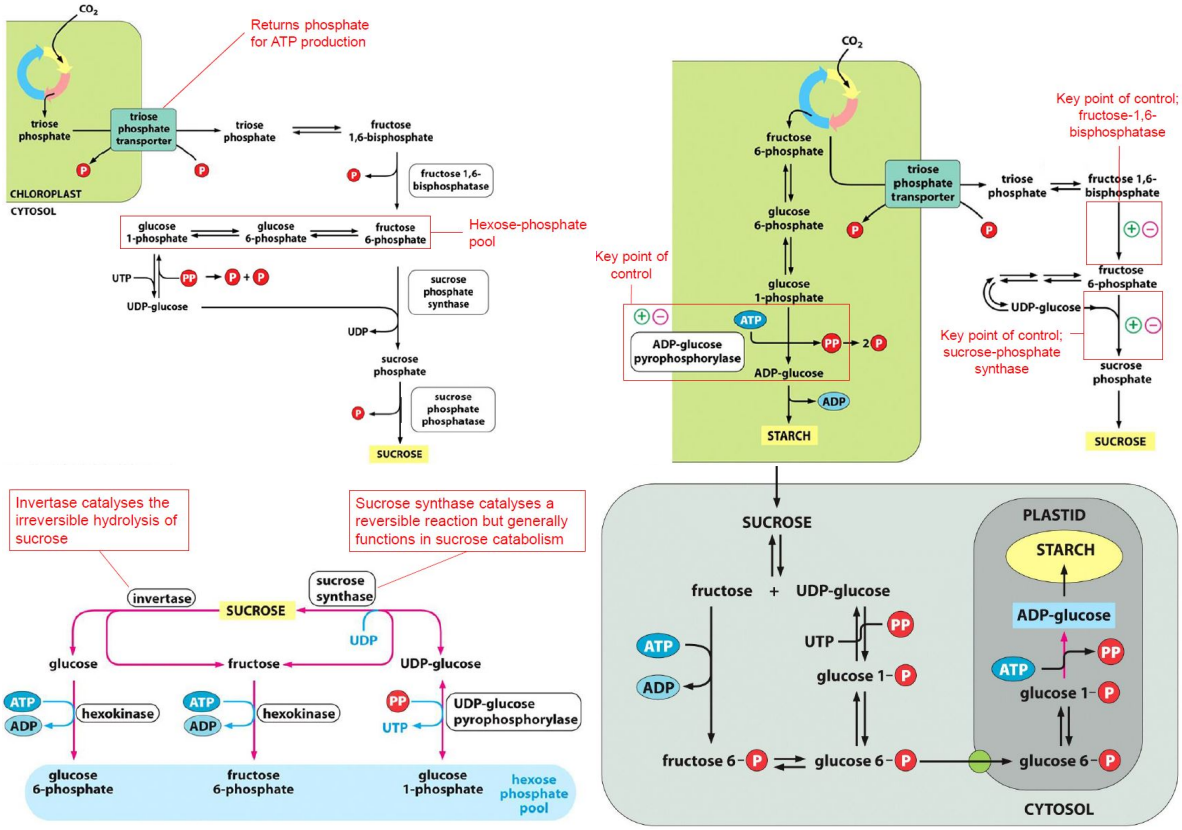
2.3 Carbohydrate Metabolism and Respiration

2.3.1 Main Products of Photosynthesis

Sucrose Metabolism: The main products of photosynthesis is sucrose, which can be stored as starch, fructans or raffinose oligosaccharides. Plants generate a much higher amount of carboydrates and thus need to assure that there are no oxidations. Sucrose is non-reducing and thus more stable and less reactive, while glucose and fructose are reducing. In fruits there are lots of glucose and fructose, but those serve as attractants of animals (sweeeter than sucrose) and fruits are on the edge of the plant anyway.
The sucrose amount is regulated by feedback regulation according to sucrose demand in non-photosynthetic tissues and feed-forward regulation by changes in the rate of carbon dioxide assimilation.
During sucrose synthesis phosphate needs to be reimported by the triose phosphate transporter into the chloroplast to form ATP. As in Glycolysis, fructose-1,6-biphosphate is the key point in regulation. The production of starch is turned up to prevent accumulation of sucrose metabolites and depletion of phosphate (starch production generates phosphate).
In sucrose metabolism there are two pathways: The invertase catalyses the irreversible hydrolysis of sucrose, while sucrose synthase catalyses a reversible reaction into fructose and UDP-glucose. During plant growth where sucrose is consumed the invertase pathway dominates, while during starch storation sucrose synthase is the more active enzyme.
During the conversion of sucrose into starch, sucrose is metabolised into glucose-6-phosphate in the cytosol. It is then transported into the plastids (while phosphate is transported into the cytosol simultaneously) where it is further converted into starch and stored in the vacuole.

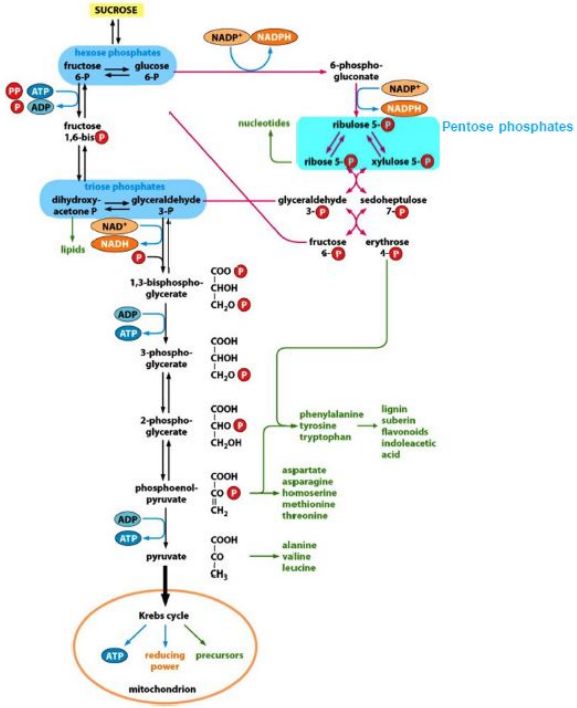
Starch Metabolism: Starch is inert and thus does not affect other reactions in the cell. During the night starch is turned into sucrose and supports the metabolism at night by yielding ATP precursors which can be fed into glycolysis and the citric acid cycle.
Starch synthase connects glucose α-1,4 and the branching enzyme introduces α-1,6 linkages. Furthermore, it promotes starch formation as it produces lose ends. Starch consists of amy-

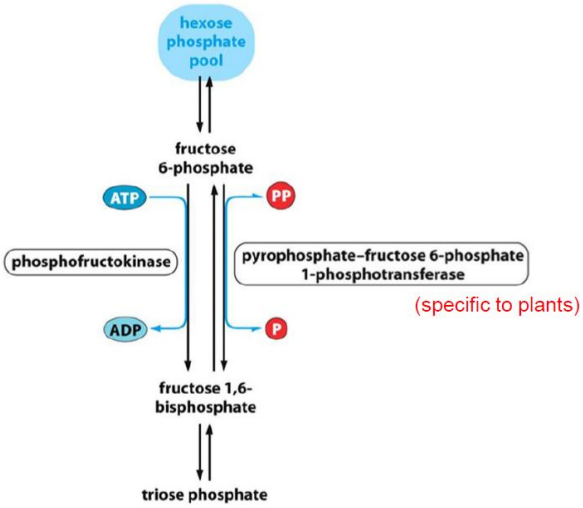
lose and amylopectin. The latter has highly-branched regions where spontanous double helix formation takes place next to regions which are unbranched (semi-crystalline zone). Amylopectin is insoluble, glycogen which is made by prokaryotes, fungi and animals, is soluble (immediately accessible for degradation). There are also debranching enzymes to ensure the correct structure is built leading to crystalisation. Amylose is synthesized within the amylopectin matrix (GBSS granule-bound starch synthase) to vary the density of starch. In starch endosperm of cereals, a gene dublication has occurred, such that ADP-glucose can be synthesised in the cytosol already.
Alternative storage products are fructan, a polymer of fructose molecules, or different variations of kestoses, Glucose with several fructose molecules attached (saccharide polymer). Raffinose-family oligosaccharides may also serve as storage product.

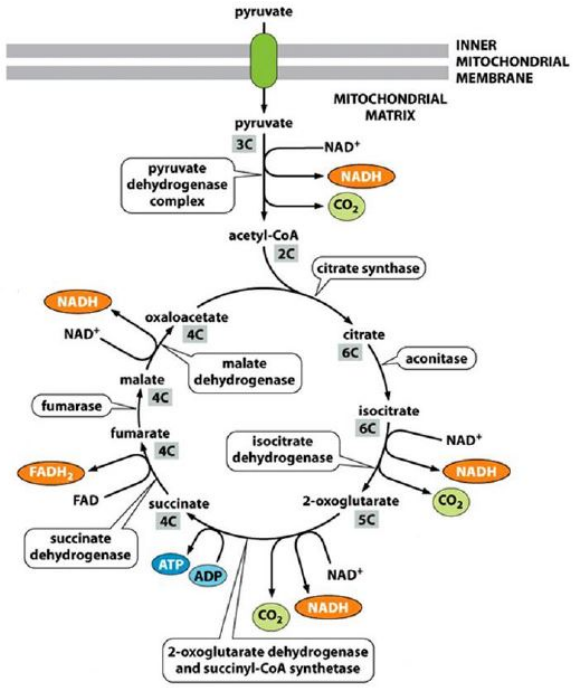


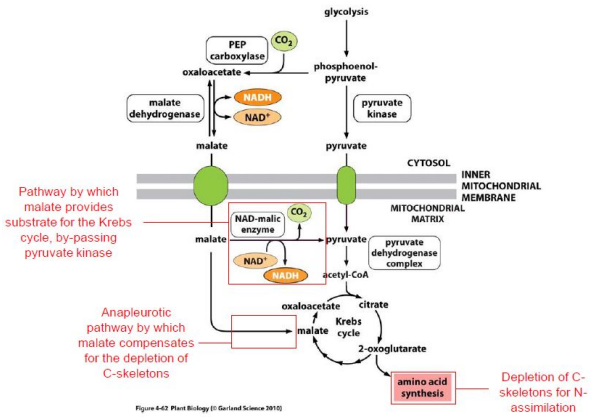
2.3.2 Respiration and Biosynthesis

Sucrose serves as substrate repiratory pathways such as glycolysis, oxidative pentose phosphate pathway and the citric acid cycle (Krebs cycle), where ATP, reducing power and biosynthetic precursors for structural, metabolic, signalling and defence biosynthesis originate.
During the day ATP levels are high, which inhibits the pyruvate kinase, therefore the malate pathway by-passes the pyruvate kinase while still providing substrates for the Krebs cycle.

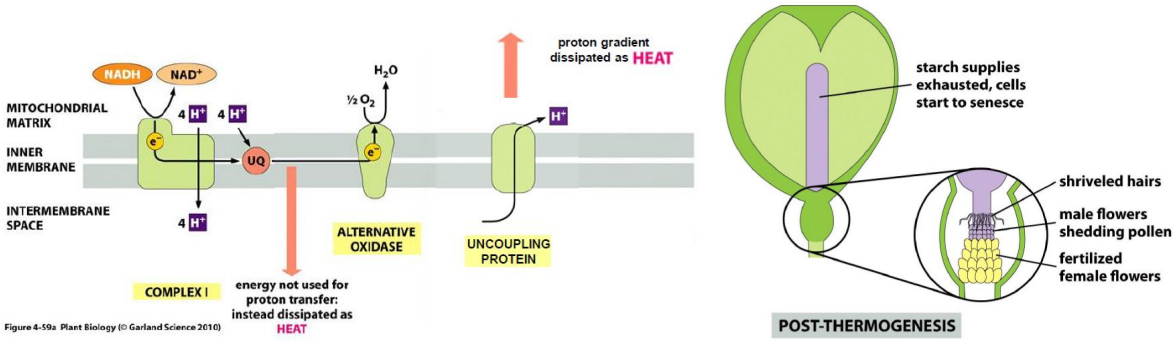








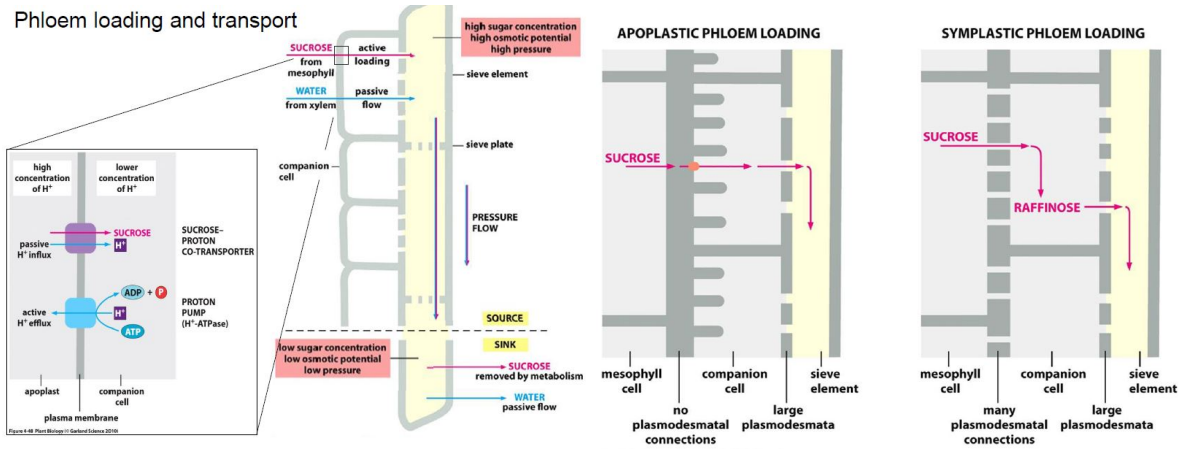
Thermogenesis: Some plants dissipate heat to spread volatile compounds to attract insects. To achieve this, massive amounts of starch are rapidly converted to PEP via glycolysis, which then enters the Krebs (citric acid) cycle. Due to the high rate of electron transport via the alternative oxidase and mitochondrial uncoupling protein a lot of heat is dissipated, that volatiles attracting compounds.



2.4 Sucrose Transport

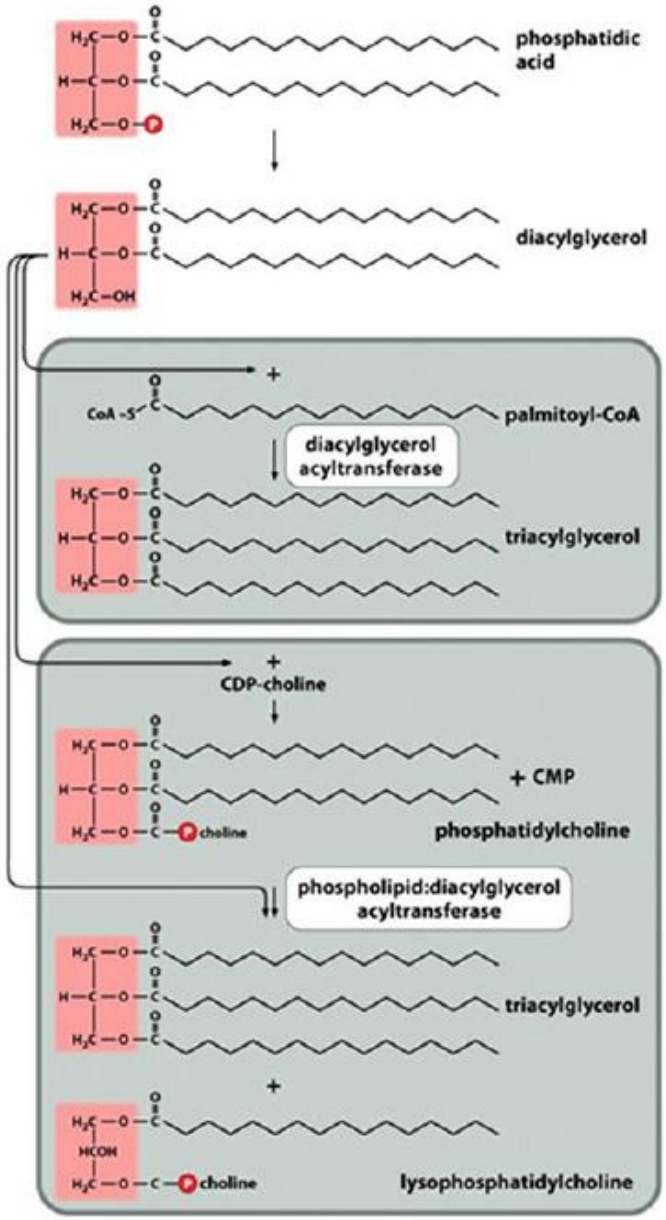
Long distance transport in plants is mediated by the vascular tissue. The phloem transports carbohydrates including sucrose, ions, small RNAs and signalling molecules from the leaves to other leaves, flowers and the root. The lignified xylem transports water and minerals from the root into the shoot. In spring, starch is transported from the root into the new leaves via the xylem. Normally these systems work due to evaporative pressure generated in the leaves: The water vapour concentration in the leaf is high while it is low in the atmosphere.

Phloem Loading and Transport: Phloem tubes are very small with thick walls to withstand the high internal pressure. Sieve cells, being kept alive by companion cells, are empty (anucleate) to allow the flow of carbohydrates. They are connected to each other via sieve plates.
Sucrose diffuses through the producing cells until to a phloem-adjacent cell, where it is loaded passively via a class of SWEET transporters into the apoplast. Then it is actively (secondary active proton coupled symport, conducted by AtSUC2 protein and driven due to proton gradient) pumped into the sieve cells (with water following the concentration gradient). Sucrose is then again removed from the sieve cells into the sink tissues which generates a pressure flow.
There is a type 1 (apoplastic loading in herbaceous species, no plasmodesmata between mesophyll and companion cells) and type 2 phloem (symplastic loading, where sucrose is converted into raffinose and then exported, not clear what drives the transport, because there is no pressure, large plasmodesmata, e.g. in trees).
In case of an injury of the phloem, the sieve plates are closed with coagulating P-protein, then a rapid cell wall synthesis follows by deposition of callose.

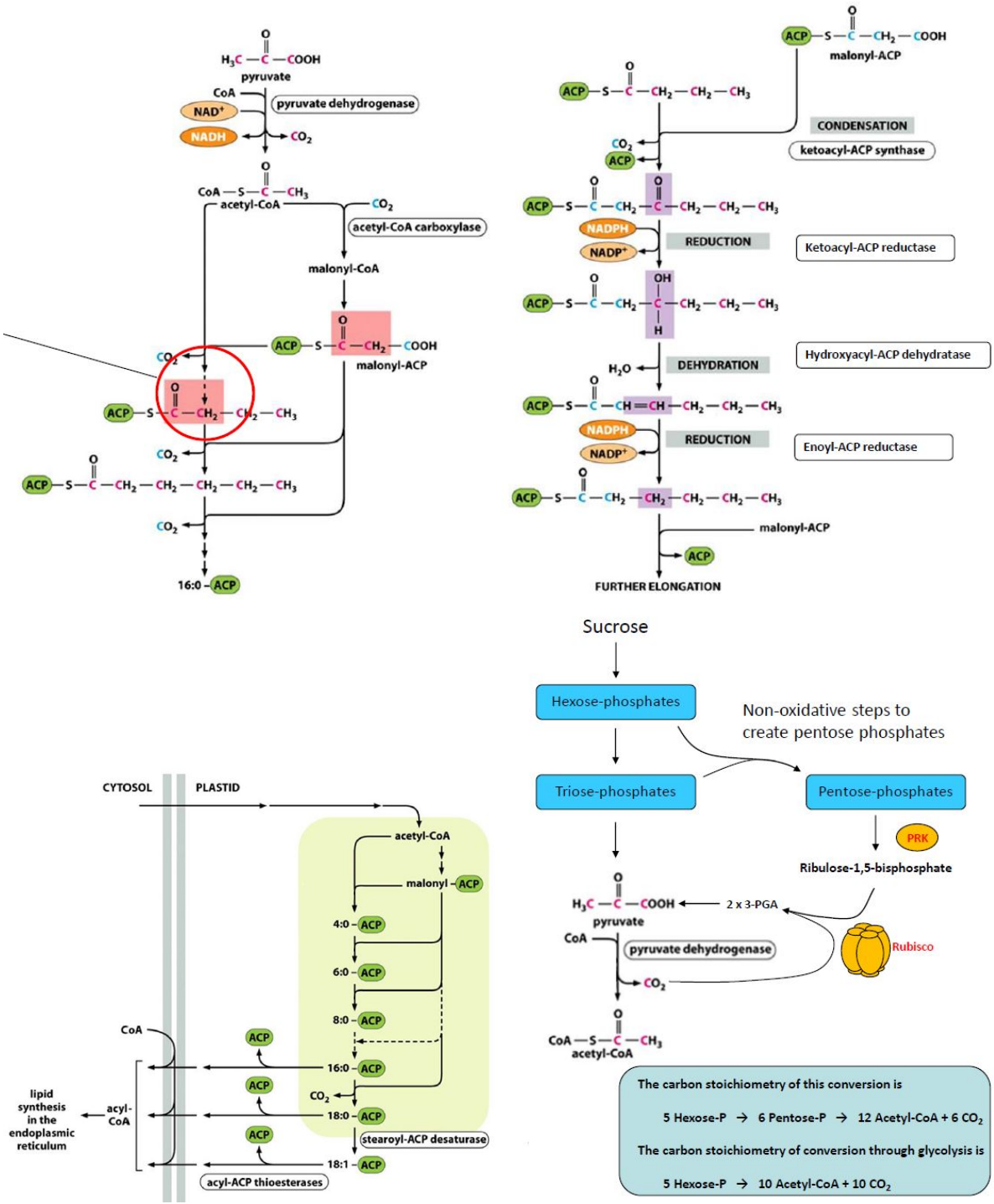


2.5 Lipid Metabolism

Triacylglycerol Synthesis: The production of triacylglycerol occurs in the ER, where the acyl transferase adds fatty acids to glycerol and fatty acid desaturases FADs introduce double bonds. There are two ways of synthesising triacylglyceroles (c.f. biochemistry). The species specific triacylglycerols accumulate in between the membrane leaflets of the ER. Oil bodies then bud off from the ER, surrounded by a phospholipid monolayer and inlaid oleosin proteins.



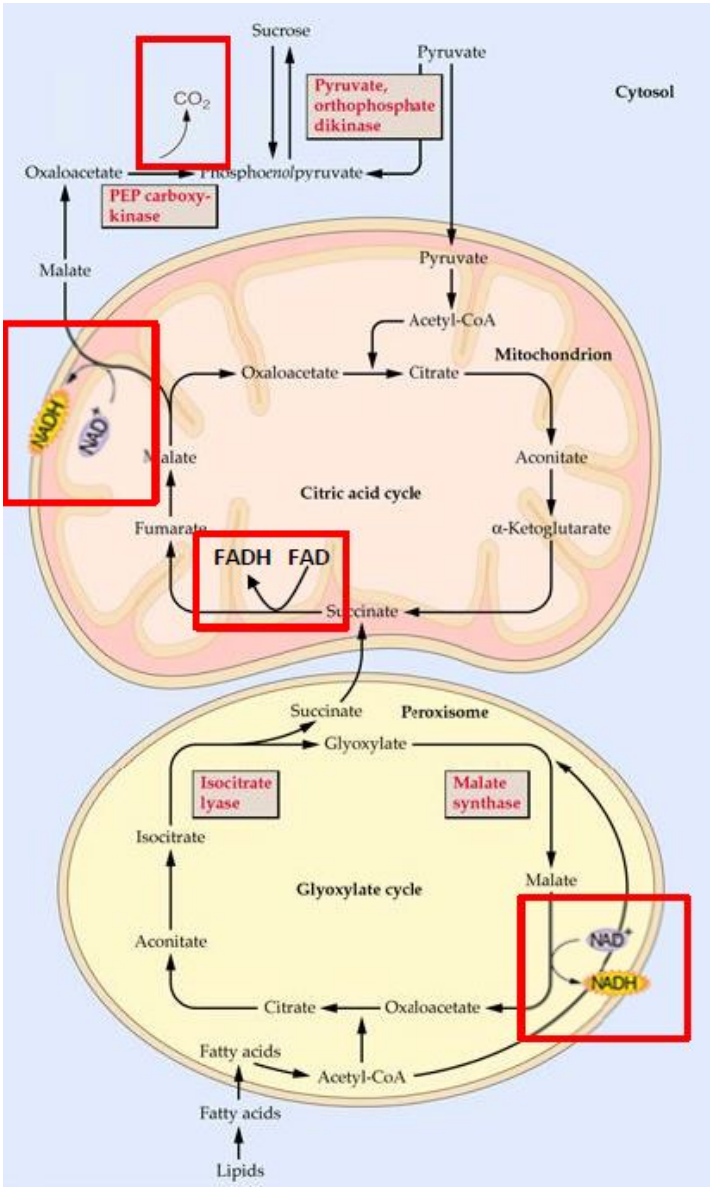
Fatty Acid Synthesis: Fatty acid (16 or 18 carbon atoms long) production starts off in the plastids from pyruvate into acetyl CoA, malonyl CoA, malonyl-ACP and eventually into a fatty acid by fatty acid synthase (red circle).
Fatty acid biosynthesis results in one third lost carbon dioxide and requires significant amounts of ATP and NADPH. The benefits outweight the costs though as energy sources of plants are not always limited. Some plant recruit phosphosynthetic enzymes to recapture otherwise lost carbon via the pentose phosphate pathway resulting in more efficiency.



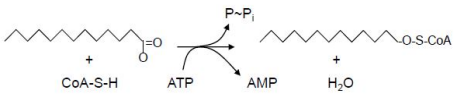
Lipid Degradation: Lipids are typically found in seeds and pollen, where they represent a store of energy and carbon for post-germination growth. They are also found in fruit and food bodies for mutualistic ants. Lipid degradation into sugars can drive enormous growth when there is no light available via three pathways: Lipolysis and β-oxidation, glyoxylate cycle and gluconeogenesis.

The process starts with lipolysis by the lipase into fatty acids and glycerol (metabolised as

triose-phosphate). The fatty acids then are imported via ABC transporter into glyoxysomes (specialised peroxisomes), where they are converted by long-chain acyl-CoA synthetase LACS into acetyl-CoA, which goes into the glyoxylate cycle. From this cycle, succinate is exported into the mitochondrion, where it is used in the citric acid cycle, being exported as malate. Malate is converted into oxalacetate, phosphoenolpyruvate and eventually into sucrose. In this process, one quarter is lost as carbon dioxide, nevertheless it is quite an efficient process (a gram-for-gram conversion of fatty acids to sugars is achieved), because some reducing power (NADH, FADH) is recaptured.



Two genes in *Arabidopsis thaliana*, LACS6 and LACS7, encode peroxisomal long-chain acyl-CoA synthetase (LACS) isozymes



Chapter 3

Prof. Olivier Voinnet

3.1 Plant Hormones I

Plant hormones are called phytohormones. As extremely high doses of hormones result in opposite effects and effects on different cell types may vary, it is hard to study them. Plants have constantly dividing stem cells. Phytohormones are not secreted in specialised organs, but sometimes in specific biosynthetic zones. Most hormones are transported in the phloem. Currently only 13 distinct plant hormones are known.
There are three main classes: Isoprenoid-derived hormones (e.g. GA), monoamine-hormones (e.g. Auxin, SA, ET) and lipid-derived hormones (e.g. JA).

3.1.1 Giberellic acid GA

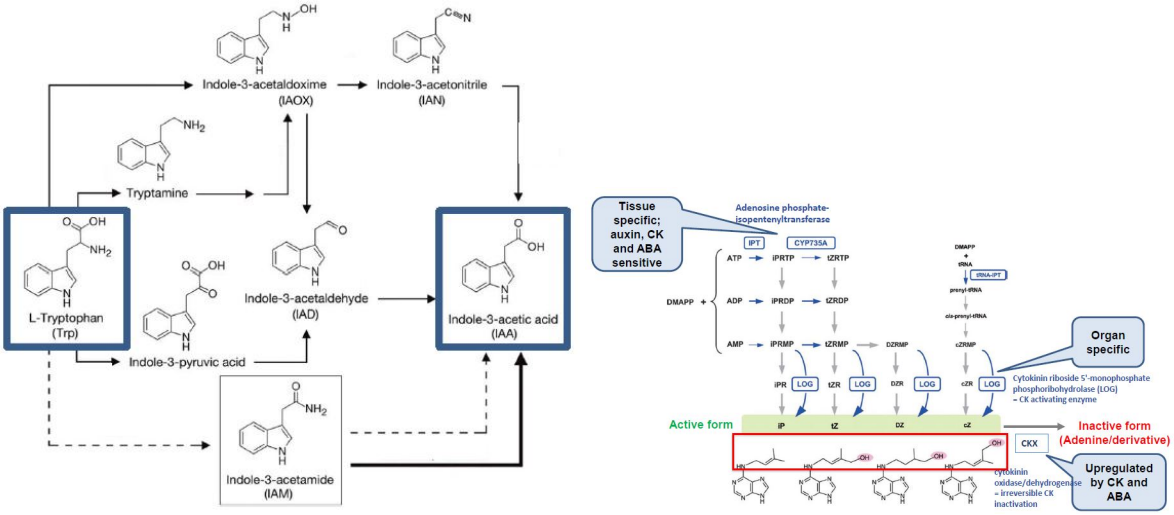
Stimulates stem elongation via cell division and elongation, flowering, breaks seed dormancy, stimulates enzyme production, sex expression and delays senescence. Biosynthesis takes place in the cytoplasm (main enzyme: dioxigenase), ER (P450 monooxigenase) and proplastids (cyclases) and is strictly regulated by light, temperature and feedback. It moves in a non-polar manner over long distances, contrary to auxin, which moves much faster from stem apex to base than in reverse direction.
Without GA present, gene transcription is inhibited, the presence of GA binding to nuclear receptor induces degradation of the DELLA inhibitor and genes are transcribed.
During seed germination GA induces synthesis of α-amylase and other hydrolases into the endosperm, which then start to degrade starch.

3.1.2 Absciic acid ABA

Biosynthesis starts from β-carotene produced in chloroplasts. Its major roles are stimulation of stomata closing and synthesis of storage proteins in seeds to avoid early germination. The process of germination is controlled by ABA and GA. During water stress (neutral pH) stabilised ABA moves from root to shoot in the xylem. Under normal acidic conditions ABA is degraded.

3.1.3 Auxin

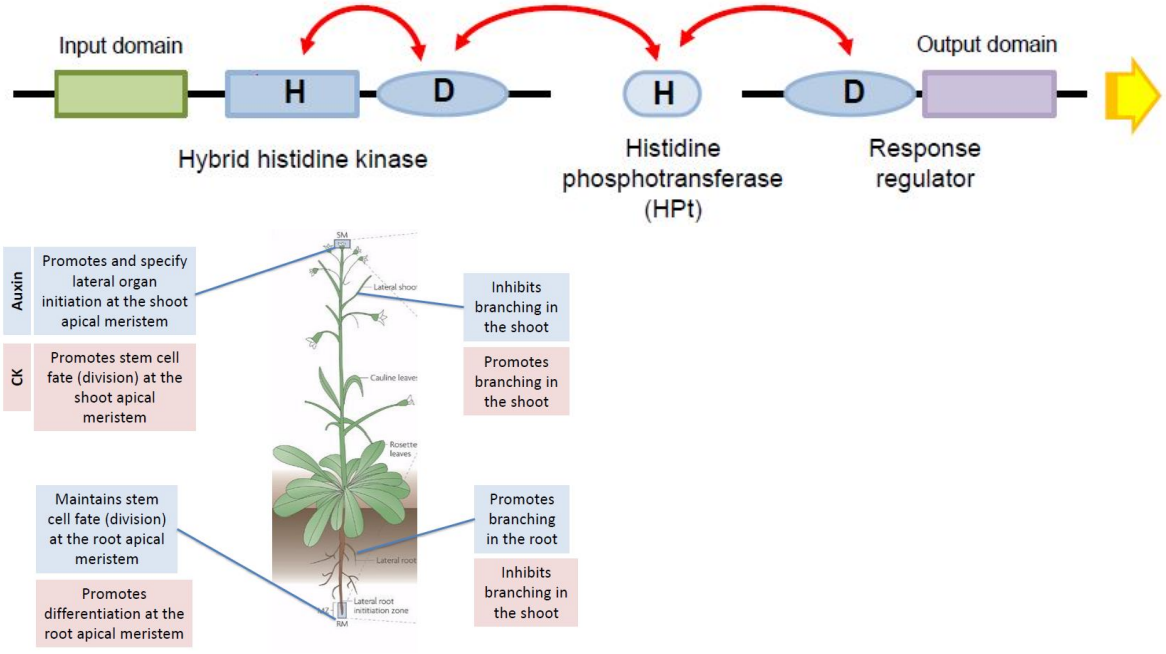
The hormone Auxin (family of indole hormones with IAA (indole-3-acetic acid) being the most abundant member) is involved in stem cell maintenance, vascular development, phototropism and gravitropism, leading to organ initiation, root and shoot branching. In phototropism, IAA accumulates on the shaded side where it stimulates elongation. Low auxin levels result in main root elongation, high levels in lateral root formation.
IAA moves trough the cells via a chemiosmotic mechanism: In the cytoplasm IAA is anionic, but in the more acidic cell wall it occurs as IAAH. The uncharged form travels the cell wall and plasma membrane into the adjacent cell where it is deprotonated and thus cannot travel any further except by specific transporters. The directionality of the transport is controlled by three families of transport proteins (one is PIN1) by asymmetric distribution of transporters. The effects of Auxin are mediated by changes in gene expression concerning genes involved in cellular growth, signalling and other hormone response pathways. During low Auxin concentration auxin-responsive-factors ARFs form a complex with Aux/IAA proteins (serve as inhibitor), which repress transcriptional activity of ARFs. If auxin concentration is high, Aux/IAA binds TIR1 receptors, which are part of the SCF ubiquitin ligase complex. Aux/IAA is degraded in the 26S proteasome and ARF induce transcription.
IAA biosynthesis occurs in the meristem from tryptophan and the involved genes are controlled by environmental and developmental factors. There are several Trp dependent pathways but also one Trp independent biosynthetic pathway.



3.1.4 Cytokinin CK

CK control cell division, leaf senescence, stem cell maintenance and auxin action (antagonist). Their primary building block is adenine and their biosynthesis is strongly regulated by positive and negative feedback, other hormones and exogenous factors. CK an Auxin together lead to cell division.
CK signalling relies on two component signalling using a hybrid histidine kinase, which transfers a phosphoryl group to a histidine phosphotranferase HPt, which then in turn mediates it to a response regulator. Depending on which transcription factor is activated by HPt, fine tuning of the CK signalling pathway is allowed.

Via antagonistic signalling of auxin and CK the two mutually exclusive domains of cellular division and differentiation in the root apex are established and maintained. They also control branching, which in turn leads to control of nutrient uptake and fruit formation.

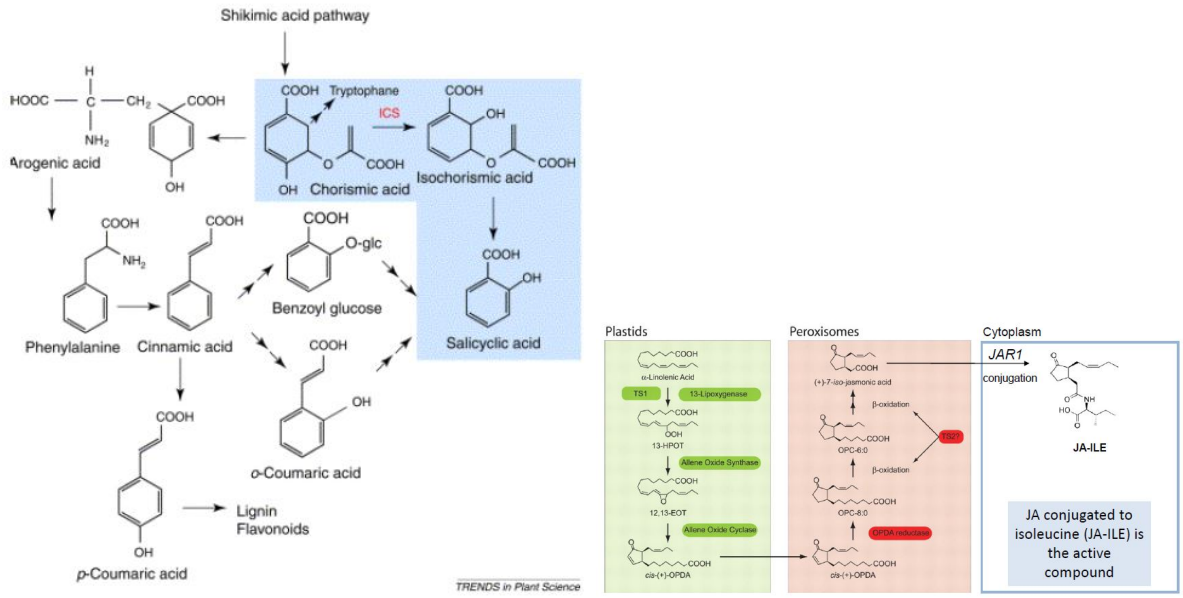


3.1.5 Ethylene

Ethylene controls fruit ripening, promotes leaf and petal senescence, controls cell division and elongation, sex determination, root growth and defence mechanisms against herbivores.
If ethylene is present it binds to the ETR1 receptor, which releases CTR kinase. The kinase inactivates itself, permitting transcription. In the absence of ethylene, CTR stays bound to the receptor and actively inhibits transcription.

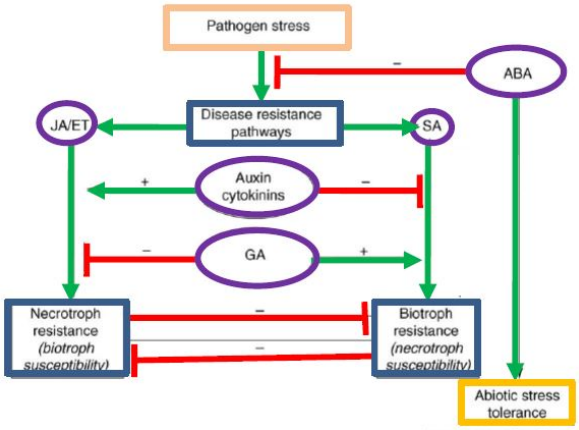
3.1.6 Salicylic Acid

Salicylic acid acts against bacteria, fungi and viruses during biotic stress, by inducing defence response and systemic acquired resistance. It is synthesised from phenylalanine, with the key enzyme isochorismate synthase ICS being activated in the chloroplasts by pathogen infection. During immune response, plants detect PAMPS pathogen associated molecular patterns such as flagellin. Recognition then triggers PAMP-triggered immunity PTI mediated by salicylic acid. Specific bacterial effector proteins can inhibit PTI, but plants exhibit resistance genes (R genes) which recognise specific bacterial effectors. If an R protein recognises an effector, a stronger immune response including the hypersensitive response HR (cell death of infected and surrounding cells to prevent spreading of pathogen) is induced. Salicylic acid is involved in transducing these signals. In the systemic acquired resistance SAR, infected sites send methyl salicylic acid MeSA and azaleic acid AzA through the vascular tissue and airborne components, making other tissues of the plant resistant to a secondary attack.



3.1.7 Jasmonic Acid

Defence against herbivores, insects, necrotrophic organisms and other animals. Biosynthesis takes place in the plastids, peroxisomes and the cytoplasm.
JA induces the secretion of anti-herbivorous chemicals including protease inhibitors. Herbivore-induced volatiles prime other tissues and plants for attack making them unpalatable. These volatiles in turn are recognised by carnivorous and parasitic insects.
If Ja-Ile is low, the JAZ protein inhibits JA-responsive-transcription-factors. With rising concentration JA-Ile binds to an F-box protein resulting in the degradation of JA-Ile, inducing transcription of defence genes. Ja and ET are both required to high-level activate ERF1, a transcription factor of defence genes.
As part of their immune response, plants modulate synthesis and response to other hormones. Some pathogens produce phytohormones (plant hormones) which interfere with hormone signalling of the plant.



3.2 Biotic Interactions

3.2.1 Biotic Stress

In wild plant populations most plants are healthy and if disease in the form of bacteria, viruses, fungi, invertebrates and other plants strikes, usually there is only a small amount of tissue or number of plants affected. Therefore, plants must have strong defence mechanisms. Growing monocultures or genetically uniform plants can lead to massive outbreaks of disease, this is why it is important to study plant pathogens.

A plant pathogen is a harmful organisms that grows at least part of his life inside a specific part of the plant. There ar several ways to invade a plant: mechanical force, enzymatic attack, natural openings as stomata, and previously wounded tissue. Once the pathogen is inside the plant it can either kill the plant by using it as substrate (necrotrophy), using it as substrate without killing the plant (biotrophy) or killing it at a later stage (hemibiotrophy). The main reasons why pathogens are successful is high rate of reproduction, efficient dispersal, spore formation at the end of the plant's season resulting in long-term survival, and high genetic diversity through sexual reproduction.

Fungal Pathogens: Some fungi produce highly host-selective toxins that are only active in a single plants species.
Biotrophic fungi penetrate the cuticula and cell wall to grow a haustorium inside the plant cell, surrounded by the plant's plasma membrane, to maximise nutrient and water uptake. They also secrete viral effectors to diminish the plant's defence response or modify plasmodesmata to ensure the haustorium's dispersal.
Hemibiotrophic pathogens switch from a biotrophic to a necrotrophic mode as nutritional demands increase.

Bacterial Pathogens: Phytobacteria often first reside within the intercellular space or in the xylem, but at some stage they start secreting toxins, EPS or cell wall degrading enzymes. Bacteria have a so called hypersensitive response and pathogenicity cluster hrp which is absolutely required for virulence. Bacterial effector proteins mainly aim to suppress PAMP triggered immunity.
Agrobacterium tumefaciens e.g. incorporates a tDNA, which encodes genes for opines (bacterial nutrition), cytokinin and auxin synthesis, into the host genome resulting in tumour growth. A disarmed tDNA is often used to produce transgenic plants.

Viral Pathogens: Phytoviruses often induce chlorosis (iron deficiency), necrosis, mosaic pattern and plant stunting. In contrast to animal viruses, plant viruses never cross the plasma membrane or cause lysis of the cells, but travel to other cells via plasmodesmata. Viruses need to enlarge plasmodesmata otherwise their RNPs would be too large.

Pathogenic Nematodes: Infections by nematodes almost always occurs via the roots, by either amphidal secretion or stylet penetration. Effector proteins cause cell division and gigantism (developing cells into a feeding factory).

Arthropodal Pathogens: Pathogenic insects can be divided into chewing and sap sucking pathogens. They also facilitate colonisation of bacterial, viral and fungal pathogens.

3.2.2 Plant Defence Systems

Reasons why most pathogens fail to infect a plant: Many plants are not able to support the demands of pathogens and thus are seen as "non-hosts".
Environmental conditions change and the pathogen dies before the infection has completed.
Some plants possess preformed structural barriers or toxic compounds. To prevent fungal penetration minute papillae made of callose and lignin form beneath the penetration site to act as a physical barrier. Fungal digestion enzymes activate plant receptors, inducing secretion of fungal cell wall digesting enzymes. Released fragments also alarm other plant receptors.
Furthermore, on recognition of the attacking pathogen defence mechanism are activated, such that the invasion remains localised. E.g. R proteins recognise effectors and induce effector-triggered immunity ETI leading to hypersensitive response HR and cell death. Plant resistance occurs only if the plants expresses the particular dominant R gene and if the pathogen expresses the complementary dominant AVIRULENCE gene AVR. If recognition cannot take place (either R gene or corresponding effector is lacking) then the plant is infected. HR kills affected cells and surrounding cells are rapidly poisoned by toxic compounds and free radicals ROS. The production of ROS involves a plasma membrane-associated NADPH oxidase. Roles of ROS in plant defence include: direct toxicity of hydrogen peroxide, signalling in SA biosynthesis, structural reinforcement of plant cell walls by cross-linking or increase of enzymatic activity in lignin polymer formation.
RNA interference is also part of the plants immune system. To combat silencing of their DNA, viruses express viral suppressors of RNA silencing VSRs.

Evolution of R Genes: As effector genes are constantly evolving due to the high reproduction rate of pathogen, plant resistance genes must somehow follow. R genes are located in R-gene clusters which permit sequence exchange generating high haplotypic diversity. Through duplications and transposons generated repeat sequences enable mispairing during recombination leading to unequal cross-overs. Intergenic unequal crossovers may alter the expression pattern while intragenic unequal crossover may generate novel function (chimeric genes). R gene clusters are conceptually equivalent to human HLA.

Systemic Plant Defense Responses: Defence responses upon recognition are activated locally within minutes. Within hours, defence is elaborated in tissues far from the infection site and even in neighbouring plants. The type of response depends on the identity of the attacking pathogen.

The bigger picture…