Plant Physiology

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Unit 1 – Plant Physiology: Cells and Introduction

1.1 Overview of plant physiology and its importance

Plant physiology uncovers the inner workings of plants, from growth to environmental responses. It's key to boosting crop yields and tackling food security challenges.

This field dives into processes like photosynthesis, water movement, and hormone actions. Understanding these helps us improve plant health and productivity in agriculture and beyond.

Introduction to Plant Physiology

Definition and Importance of Plant Physiology

- Plant physiology studies the functions, processes, and mechanisms within plants
- Encompasses how plants grow, develop, and respond to their environment
- Crucial for understanding how plants survive, adapt, and reproduce
- Provides insights into how to optimize plant growth and productivity for agriculture, horticulture, and forestry

Autotrophs and Photosynthesis

- Plants are autotrophs, organisms that produce their own food using inorganic compounds
- Photosynthesis is the process plants use to convert light energy into chemical energy stored in glucose
- During photosynthesis, plants use carbon dioxide, water, and light energy to produce glucose and oxygen
- Photosynthesis occurs primarily in the leaves, specifically in chloroplasts containing chlorophyll
- The two main stages of photosynthesis are the light-dependent reactions (light reaction) and the light-independent reactions (Calvin cycle)

Transpiration and Water Movement

- Transpiration is the loss of water vapor from plants through stomata in the leaves
- Drives the movement of water and nutrients from the roots to the leaves through the xylem
- Helps cool the plant and maintains cell turgor pressure
- Factors affecting transpiration include temperature, humidity, wind, and light intensity
- Guard cells regulate the opening and closing of stomata to control transpiration and gas exchange (carbon dioxide and oxygen)

Plant Growth and Development

Phytohormones and Their Functions

- Phytohormones are chemical messengers that regulate plant growth, development, and responses to stimuli
- Auxins stimulate cell elongation, root formation, and apical dominance (suppression of lateral bud growth)
- Cytokinins promote cell division, delay leaf senescence, and stimulate shoot branching
- Gibberellins stimulate stem elongation, seed germination, and fruit development
- Abscisic acid (ABA) regulates stomatal closure, seed dormancy, and stress responses (drought and cold)
- Ethylene is a gaseous hormone that promotes fruit ripening, leaf abscission, and senescence

Applied Plant Physiology

Biotechnology and Genetic Engineering

- Biotechnology applies biological processes, organisms, or systems to develop products or technologies
- Genetic engineering involves modifying the genetic material (DNA) of plants to introduce desirable traits
- Examples of genetically modified (GM) crops include herbicide-resistant soybeans, insect-resistant corn, and vitamin A-enriched golden rice
- Biotechnology techniques include tissue culture, marker-assisted selection, and genetic transformation (using Agrobacterium or gene guns)
- Benefits of biotechnology include increased crop yield, improved nutritional value, and enhanced resistance to pests and diseases

Crop Improvement and Sustainable Agriculture

- Crop improvement aims to develop plant varieties with desirable traits such as high yield, disease resistance, and stress tolerance
- Conventional breeding methods involve crossing plants with desired traits and selecting the best offspring over multiple generations
- Modern techniques include hybrid breeding, mutation breeding, and marker-assisted selection
- Sustainable agriculture practices aim to maintain soil health, conserve water, and minimize the use of synthetic fertilizers and pesticides
- Examples of sustainable practices include crop rotation, intercropping, cover cropping, and integrated pest management (IPM)
- Precision agriculture uses technology (GPS, sensors, and drones) to optimize resource use and minimize environmental impact

1.2 Plant cell structure and function

Plant cells are complex structures with unique features that set them apart from animal cells. Their specialized components, like the cell wall and chloroplasts, enable plants to perform photosynthesis and maintain structural integrity in diverse environments.

The cell membrane, organelles, and cytoskeleton work together to support vital plant functions. Understanding these structures is crucial for grasping how plants grow, respond to stimuli, and adapt to their surroundings.

Cell Membrane and Wall

Cell Wall Structure and Function

- Provides structural support and protection to the plant cell
- Composed primarily of cellulose, a complex carbohydrate polymer
- Cellulose microfibrils are arranged in a crisscross pattern, providing strength and flexibility
- Additional components include hemicellulose, pectin, and lignin (in secondary cell walls)
- Allows for the passage of water and small molecules through pores

Plasma Membrane Composition and Role

- Selectively permeable barrier that surrounds the cell, regulating the movement of substances in and out
- Composed of a phospholipid bilayer with embedded proteins
- Phospholipids have hydrophilic heads and hydrophobic tails, forming a stable barrier
- Integral proteins span the membrane and facilitate transport (channels, carriers, pumps)
- Peripheral proteins are attached to the surface and serve various functions (enzymes, receptors)

Plasmodesmata: Intercellular Communication

- Channels that connect the cytoplasm of adjacent plant cells through the cell walls
- Allows for the direct exchange of small molecules, ions, and signaling molecules between cells
- Plays a crucial role in cell-to-cell communication and coordination of plant processes
- Consists of a plasma membrane-lined channel with a central strand of endoplasmic reticulum (desmotubule)
- Size exclusion limit (SEL) determines the maximum size of molecules that can pass through plasmodesmata

Organelles

Chloroplast: Photosynthesis Powerhouse

- Organelle responsible for photosynthesis, converting light energy into chemical energy
- Contains chlorophyll pigments that absorb light energy (primarily in the blue and red wavelengths)

- Consists of a double membrane, thylakoid membranes (site of light-dependent reactions), and stroma (site of light-independent reactions)
- Thylakoid membranes are arranged in stacks called grana, connected by unstacked regions (stroma lamellae)
- Produces glucose and oxygen as end products of photosynthesis

Mitochondria: Cellular Respiration Hub

- Organelle responsible for cellular respiration, generating ATP (energy currency) from the breakdown of organic molecules
- Consists of a double membrane, with the inner membrane folded into cristae to increase surface area
- Matrix contains enzymes involved in the citric acid cycle (Krebs cycle)
- Electron transport chain (ETC) and ATP synthase are located in the inner membrane
- Produces ATP, carbon dioxide, and water as end products of cellular respiration

Endomembrane System: Synthesis, Modification, and Transport

- Endoplasmic Reticulum (ER): Network of membrane-bound channels and sacs involved in protein and lipid synthesis
- Rough ER has ribosomes attached and synthesizes proteins for secretion or membrane insertion
- Smooth ER lacks ribosomes and functions in lipid synthesis, detoxification, and calcium storage
- Golgi Apparatus: Modifies, packages, and sorts proteins and lipids received from the ER
- Consists of a stack of flattened membrane sacs (cisternae) with a cis face (receiving) and a trans face (shipping)
- Modifies proteins through glycosylation, phosphorylation, and other post-translational modifications
- Packages molecules into vesicles for transport to other organelles or secretion from the cell

Vacuole: Storage and Turgor Pressure Maintenance

- Large, membrane-bound organelle that occupies most of the cell volume in mature plant cells
- Functions in storage of water, ions, metabolites, and waste products
- Maintains turgor pressure, which provides structural support and enables cell elongation
- Contains hydrolytic enzymes for the breakdown of macromolecules and recycling of cell components
- In some specialized cells, vacuoles store pigments (anthocyanins) or defensive compounds

Cell Structure

Cytoskeleton: Cellular Scaffolding and Movement

- Network of protein filaments that provide structure, support, and movement within the cell
- Consists of three main components: microfilaments, intermediate filaments, and microtubules

- Microfilaments (actin filaments) are involved in cell shape, movement, and cytoplasmic streaming
- Composed of actin monomers that polymerize into thin, flexible filaments
- Associated with myosin motor proteins for movement and transport
- Intermediate filaments provide mechanical strength and resistance to mechanical stress
- Composed of various proteins, such as keratins and lamins
- Help maintain the integrity of the cell and its organelles
- Microtubules are hollow, cylindrical structures involved in cell division, organelle positioning, and cell wall deposition
- Composed of α- and β-tubulin dimers that polymerize into long, rigid filaments
- Organize into the mitotic spindle during cell division, separating chromosomes
- Serve as tracks for motor proteins (kinesins and dyneins) to transport organelles and vesicles

1.3 Membrane transport and cellular communication

Membrane transport and cellular communication are crucial for plant survival. These processes allow plants to move nutrients, regulate water balance, and respond to environmental cues. From passive diffusion to energy-driven active transport, plants use various mechanisms to maintain cellular homeostasis.

Plants rely on complex signaling pathways to communicate within and between cells. These pathways involve receptors, signaling molecules, and transduction cascades that enable plants to sense and respond to their environment. Understanding these processes is key to grasping plant physiology and cell biology.

Passive Membrane Transport

Movement of molecules across membranes

- Diffusion is the movement of molecules from an area of high concentration to an area of low concentration down a concentration gradient
- Osmosis is the movement of water across a semipermeable membrane from an area of high water potential to an area of low water potential
- Water moves from a hypotonic solution to a hypertonic solution across a selectively permeable membrane
- Osmotic pressure is the minimum pressure required to prevent the inward flow of water across a semipermeable membrane
- Facilitated diffusion is the movement of molecules across a membrane with the assistance of transport proteins
- Allows for the movement of larger or charged molecules that cannot pass through the membrane on their own (glucose, amino acids)

Specialized channels for transport

- Ion channels are protein pores in the membrane that allow specific ions to pass through

- Gated ion channels open or close in response to a stimulus such as a change in voltage or ligand binding
- Examples include potassium channels, sodium channels, and calcium channels
- Aquaporins are water channel proteins that facilitate the rapid movement of water across cell membranes
- Play a crucial role in maintaining water balance in cells and tissues (root hair cells, guard cells)
- Aquaporins can be regulated by phosphorylation or pH changes to control water flow

Active Membrane Transport

Energy-dependent transport processes

- Active transport is the movement of molecules against their concentration gradient using energy from ATP
- Primary active transport directly uses ATP to power the transport of molecules (sodium-potassium pump, proton pumps in plant vacuoles)
- Secondary active transport uses the electrochemical gradient created by primary active transport to move molecules against their concentration gradient (sodium-glucose cotransporter)
- The symplast is the continuous system of cytoplasm connected by plasmodesmata that allows for the transport of molecules between cells
- Plasmodesmata are channels that connect the cytoplasm of adjacent cells, allowing for intercellular communication and transport

Apoplastic transport

- The apoplast is the continuous system of cell walls and intercellular spaces that allows for the transport of water and solutes external to the cells
- Water and dissolved minerals move through the apoplast of root cells before entering the symplast
- Apoplastic transport is driven by transpiration, which creates a water potential gradient that pulls water and solutes up through the xylem

Cellular Communication

Signal transduction components

- Signal transduction is the process by which cells convert external signals into cellular responses
- Involves the binding of a signaling molecule to a receptor, which initiates a series of biochemical reactions that ultimately lead to a cellular response
- Receptors are proteins that bind to specific signaling molecules and initiate signal transduction pathways
- Cell surface receptors are located on the plasma membrane and bind to extracellular signaling molecules (receptor kinases, G protein-coupled receptors)

- Intracellular receptors are located within the cell and bind to signaling molecules that can pass through the membrane (steroid hormone receptors)

Signaling molecules and pathways

- Signaling molecules are chemical compounds that convey information between cells or within a cell
- Examples include hormones (auxins, cytokinins), neurotransmitters, and growth factors
- Signaling molecules can act locally (paracrine signaling) or over long distances (endocrine signaling)
- Transduction pathways are series of biochemical reactions that relay the signal from the receptor to the target molecule, often involving second messengers and protein kinases
- Second messengers are small molecules that amplify and propagate the signal within the cell (cyclic AMP, calcium ions)
- Protein kinases are enzymes that phosphorylate target proteins, modulating their activity and leading to cellular responses (MAP kinases, CDPKs in plants)

1.4 Plant genomics and molecular biology techniques

Plant genomics and molecular biology techniques are essential tools for understanding plant physiology. These methods allow scientists to study genes, modify genomes, and analyze gene expression, providing insights into plant function and development.

From DNA sequencing to CRISPR gene editing, these techniques have revolutionized plant research. They enable the creation of improved crops and help unravel the complexities of plant biology, connecting molecular processes to broader physiological functions.

Genomic Analysis Techniques

DNA Sequencing and Amplification

- DNA sequencing determines the precise order of nucleotides within a DNA molecule
- Enables researchers to identify genes, regulatory sequences, and other important genomic features
- Common methods include Sanger sequencing and next-generation sequencing (Illumina, PacBio)
- Polymerase chain reaction (PCR) amplifies specific DNA sequences
- Uses a thermal cycler to repeatedly denature, anneal, and extend DNA strands
- Requires primers complementary to the target sequence, DNA polymerase, and nucleotides
- Allows for the rapid generation of millions of copies of a specific DNA fragment (amplicons)

Bioinformatics Tools and Databases

- Bioinformatics involves the use of computational tools to analyze and interpret biological data
- Enables researchers to process and make sense of large genomic datasets
- Includes sequence alignment, gene prediction, and phylogenetic analysis
- Genomic databases store and organize DNA sequences and annotations
- Examples include GenBank, Ensembl, and Phytozome for plant genomes

- Provide access to reference genomes, gene models, and functional annotations

Genetic Modification Methods

Genetic Engineering Techniques

- Genetic engineering involves the direct manipulation of an organism's genome
- Enables the introduction of new genes or modification of existing ones
- Common methods include Agrobacterium-mediated transformation and particle bombardment
- Transgenic plants contain genes from other species
- Allow for the introduction of novel traits (herbicide resistance, insect resistance)
- Require proper regulation and safety assessment before commercialization

CRISPR-Cas9 Gene Editing

- CRISPR-Cas9 is a precise gene editing tool adapted from bacterial immune systems
- Uses a guide RNA to target specific DNA sequences and a Cas9 endonuclease to create double-strand breaks
- Allows for the introduction of targeted mutations or insertion of new sequences
- CRISPR-Cas9 has revolutionized plant genome editing
- Enables the rapid generation of knockout mutants and precise gene modifications
- Has potential applications in crop improvement (disease resistance, yield enhancement)

Gene Expression Studies

Measuring Gene Expression Levels

- Gene expression refers to the process by which information from a gene is used to synthesize functional gene products (RNA and proteins)
- Studying gene expression patterns can provide insights into gene function and regulation
- Common methods for measuring gene expression include microarrays, RNA-seq, and quantitative PCR (qPCR)
- Microarrays measure the expression levels of thousands of genes simultaneously
- Use DNA probes attached to a solid surface to hybridize with fluorescently labeled cDNA or cRNA
- Allow for the comparison of gene expression profiles between different samples or conditions

High-Throughput RNA Sequencing (RNA-seq)

- RNA-seq uses next-generation sequencing to quantify gene expression
- Involves converting RNA to cDNA, fragmenting, and sequencing
- Provides a more comprehensive and unbiased view of the transcriptome compared to microarrays

- RNA-seq data analysis involves mapping reads to a reference genome, quantifying gene expression, and identifying differentially expressed genes
- Enables the discovery of novel transcripts and alternative splicing events
- Can be used to study gene expression changes in response to environmental stresses or developmental stages

Quantitative PCR (qPCR) for Targeted Gene Expression Analysis

- Quantitative PCR (qPCR) measures the amplification of a target gene in real-time
- Uses fluorescent dyes or probes to detect the accumulation of PCR products
- Allows for the precise quantification of gene expression levels
- qPCR is often used to validate results from microarrays or RNA-seq experiments
- Requires careful design of primers and selection of reference genes for normalization
- Provides a sensitive and specific method for studying the expression of individual genes

Unit 2 – Plant Water & Mineral Nutrition

2.1 Water potential and plant-water relations

Water Potential and Components

Water potential is the central concept for understanding how water moves through plants. It quantifies the tendency of water to move from one location to another, and that movement governs everything from cell turgor to long-distance transport in the xylem. Once you understand water potential and its components, the rest of plant-water relations falls into place.

Measuring Water Potential

Water potential (Ψ) measures the free energy of water in a system relative to pure water at atmospheric pressure. Water always moves from regions of higher water potential to regions of lower water potential.

- Pure water at atmospheric pressure and no elevation difference defines $\Psi = 0$ MPa. Any factor that reduces water's free energy makes Ψ negative.
- The full equation for a plant cell is: $\Psi = \Psi_s + \Psi_p$, where Ψ_s is osmotic (solute) potential and Ψ_p is pressure potential. (Matric and gravitational components matter in soil and tall trees but are often simplified out at the cell level.)

Osmotic potential (Ψ_s) captures the effect of dissolved solutes. Solutes lower the free energy of water, so Ψ_s is always zero or negative.

- Calculated with the van't Hoff equation: $\Psi_s = -iCRT$
- i = ionization constant (number of particles the solute dissociates into; for sucrose, $i = 1$; for NaCl, $i = 2$)
- C = molar concentration of the solute
- R = ideal gas constant (0.00831 $L \cdot MPa \cdot mol^{-1} \cdot K^{-1}$)
- T = absolute temperature in Kelvin
- A 0.1 M sucrose solution at 25 °C (298 K) gives $\Psi_s = -(1)(0.1)(0.00831)(298) \approx -0.25$ MPa. Adding more solute makes Ψ_s more negative.

Pressure and Turgor

Pressure potential (Ψ_p) is the hydrostatic pressure exerted on or by water in a system.

- In a turgid plant cell, the rigid cell wall pushes back against the expanding protoplast, creating a positive Ψ_p that raises the cell's overall water potential.
- In the xylem during transpiration, tension (negative hydrostatic pressure) develops, so Ψ_p can be strongly negative there.
- Root pressure is an example of positive Ψ_p generated in root xylem, sometimes visible as guttation droplets on leaf margins at night.

Turgor pressure is the specific case of Ψ_p inside a living plant cell. When water enters a cell by osmosis (because Ψ_s inside is more negative than outside), the cell contents press outward against the cell wall.

This pressure keeps cells firm and drives cell expansion during growth. When turgor drops to zero, the cell is flaccid and the plant wilts.

Plasmolysis occurs when a cell is placed in a hypertonic solution (external Ψ_s more negative than internal). Water leaves the cell, the plasma membrane pulls away from the cell wall, and the cytoplasm shrinks. Incipient plasmolysis, the point where the membrane just begins to detach, is when $\Psi_p = 0$ and $\Psi_{cell} = \Psi_s$. Prolonged plasmolysis can kill the cell because membrane integrity is lost.

Soil Water and Plant Interactions

Soil Water Availability

Not all water in soil is available to plants. Two benchmarks define the usable range:

- Field capacity is the water content remaining after a saturated soil has drained freely under gravity (typically around -0.033 MPa). This is the upper limit of water available to roots. Soil texture matters: clay soils hold more water at field capacity than sandy soils because their smaller pore spaces retain water more tightly.
- Permanent wilting point is the soil water potential at which roots can no longer extract water, roughly -1.5 MPa for most crop species. Below this threshold, the remaining water is held too tightly by soil particles for root uptake, and the plant wilts irreversibly.

The difference between field capacity and permanent wilting point is called plant-available water. Loam soils tend to have the most plant-available water because they balance drainage with water retention.

Transpiration and Plant Water Loss

Transpiration is the evaporation of water from leaf surfaces, primarily through open stomata. It is the main driver of long-distance water movement in plants.

The water potential gradient that powers transpiration is steep. Leaf air spaces may have a water potential of -100 MPa or lower on a dry day, while soil water sits near -0.01 to -0.5 MPa. Water flows down this gradient: soil → root → xylem → leaf → atmosphere.

Factors that increase transpiration rate: - Higher temperature increases the vapor pressure inside the leaf relative to outside air. - Lower humidity steepens the vapor pressure gradient between leaf and atmosphere. - Wind removes the boundary layer of humid air around the leaf surface. - Higher light intensity triggers stomatal opening (stomata open in response to blue light and low internal CO_2).

On a hot, dry, windy day all four factors combine, and transpiration rates can be very high. Plants regulate this by closing stomata, but that also limits CO_2 uptake for photosynthesis, creating a fundamental trade-off.

Water Transport in Plants

Cohesion-Tension Theory

The cohesion-tension theory is the accepted explanation for how water ascends the xylem, even in trees over 100 m tall. It relies on three physical properties:

1. Transpiration creates tension. As water evaporates from mesophyll cell walls into leaf air spaces, the menisci in the tiny cell-wall pores generate very negative pressures (tension) due to surface tension.

2. Cohesion maintains a continuous water column. Water molecules are linked by hydrogen bonds, giving liquid water high tensile strength. This means the column can be pulled from above without breaking easily.

3. Adhesion assists the column. Water molecules also adhere to the hydrophilic, lignified walls of xylem conduits, helping counteract gravity and preventing the column from pulling away from the walls.

The result is a continuous "chain" of water from root to leaf. Tension generated at the top is transmitted all the way down to the roots, lowering water potential in root xylem and drawing water in from the soil. No metabolic energy is spent on this transport; it is entirely driven by the evaporative demand of the atmosphere.

Cavitation risk: If tension becomes too great (during severe drought, for example), dissolved gas can come out of solution and form an air bubble (embolism) that breaks the water column in that conduit. Plants have mechanisms to limit the spread of embolisms, including pit membranes between adjacent conduits and, in some species, the ability to refill embolized vessels via root pressure overnight.

Xylem Structure and Function

Xylem is the vascular tissue that transports water and dissolved minerals from roots to shoots. It also provides structural support because of its lignified cell walls.

Two main conducting cell types make up xylem:

- Tracheids are elongated cells with tapered, overlapping ends. Water passes between tracheids through pit pairs (thin regions in the wall). Tracheids are found in all vascular plants, including ferns and gymnosperms. Their narrow diameter and pit membranes make them more resistant to embolism spread but also slower conductors.

- Vessel elements are shorter, wider cells stacked end-to-end with perforated end walls (perforation plates), forming continuous tubes called vessels. They conduct water much more efficiently than tracheids due to their larger diameter and open connections. Vessel elements are characteristic of angiosperms, though a few gymnosperm lineages also have them.

Xylem transport is a passive process. No ATP is required. The driving force is the water potential gradient from soil to atmosphere:

$\Psi_{soil} > \Psi_{root} > \Psi_{xylem} > \Psi_{leaf} > \Psi_{atmosphere}$

In a tall tree, water must be pulled upward against gravity (gravity reduces Ψ by about 0.01 MPa per meter of height) and must overcome frictional resistance inside the conduits. The cohesion-tension mechanism generates enough force to accomplish this because the atmospheric demand can produce tensions of -2 MPa or more in the xylem, far exceeding what gravity and friction impose.

2.2 Soil-plant-atmosphere continuum

Water movement in plants is a complex process involving the soil-plant-atmosphere continuum. This system describes how water travels from the soil through plants and into the air, driven by water potential gradients and various plant structures.

Factors like hydraulic conductivity, root pressure, and leaf water potential affect water movement. Understanding these processes is crucial for grasping how plants manage water, which is essential for their growth, survival, and adaptation to different environments.

Water Movement in the SPAC

Soil-Plant-Atmosphere Continuum (SPAC)

• Describes the continuous pathway of water movement from the soil through plants and into the atmosphere

• Water moves through the SPAC along a water potential gradient, always moving from areas of high water potential to areas of low water potential

• Major components include soil water, root water uptake, xylem transport, leaf evaporation, and atmospheric humidity

• Water movement is driven by the combined forces of adhesion (water molecules sticking to xylem walls) and cohesion (water molecules sticking to each other)

Factors Affecting Water Movement

• Hydraulic conductivity measures the ease with which water moves through the plant's vascular system (xylem)

• Influenced by xylem vessel diameter, length, and presence of obstructions (tyloses or air bubbles)

• Higher hydraulic conductivity allows for more efficient water transport from roots to leaves (maize vs. sugarcane)

• Root pressure is the positive pressure that develops in the xylem sap of the root system, helping to push water upward

• Generated by active transport of ions into the xylem, which creates an osmotic gradient that draws water in (guttation in strawberries)

• Leaf water potential is a measure of the free energy of water in the leaf cells

• More negative values indicate higher water stress and a greater pull on water from the xylem (wilted vs. turgid leaves)

Transpiration and Stomata

Stomatal Regulation of Transpiration

• Stomatal conductance refers to the degree of stomatal opening and the ease with which water vapor and CO_2 can diffuse through the stomata

• Regulated by guard cells, which open and close stomata in response to environmental cues (light, humidity, CO_2 concentration)

• Higher stomatal conductance leads to increased transpiration rates and greater water loss from leaves (desert plants vs. tropical plants)

• Transpiration is the loss of water vapor from plant leaves through stomata

• Serves important functions such as cooling leaves, maintaining water and nutrient uptake, and facilitating carbon dioxide entry for photosynthesis

• Rate is influenced by factors such as temperature, wind speed, and relative humidity

Vapor Pressure Deficit (VPD)

- VPD is the difference between the amount of moisture in the air and the amount of moisture the air can hold when saturated
- Higher VPD indicates drier air and a steeper gradient for water loss from leaves to the atmosphere
- Plants may close stomata in response to high VPD to reduce water loss and prevent dehydration (midday depression in photosynthesis)
- Transpiration rates are directly proportional to the VPD between the leaf and the surrounding air
- As VPD increases, the rate of water loss from leaves also increases, unless stomatal conductance is reduced

Xylem Dysfunction

Cavitation and Embolism Formation

- Cavitation is the formation of air bubbles in the xylem vessels under conditions of high tension or freezing
- Occurs when the water column is stretched to the point where dissolved air comes out of solution and forms bubbles
- Can be caused by drought stress, freezing temperatures, or mechanical damage to xylem vessels
- Embolism refers to the blockage of xylem vessels by air bubbles, preventing water flow
- As more vessels become embolized, the hydraulic conductivity of the xylem decreases, limiting water transport to leaves
- Severe embolism can lead to leaf desiccation, wilting, and ultimately plant death (pine trees affected by bark beetles)

Consequences and Adaptations

- Xylem dysfunction due to cavitation and embolism can have significant impacts on plant water relations and survival
- Reduced hydraulic conductivity limits water supply to leaves, leading to stomatal closure, reduced photosynthesis, and impaired growth
- Plants may exhibit leaf shedding, branch dieback, or mortality under severe or prolonged water stress (drought-induced tree mortality)
- Some plants have evolved adaptations to minimize the risk of xylem dysfunction or to recover from embolism
- Narrow xylem vessels, thicker cell walls, and intervessel pits with smaller apertures can reduce the likelihood of cavitation (desert shrubs)
- Some species can refill embolized vessels through the generation of positive root pressure or the release of sugars into the xylem sap (grapevines)

2.3 Mineral uptake and transport

Mineral uptake and transport are crucial processes for plant survival. Plants use active and passive transport mechanisms to move essential minerals from the soil into their roots. Ion channels and carrier proteins play key roles in facilitating this movement across cell membranes.

Once inside the roots, minerals travel through symplastic and apoplastic pathways. The Casparian strip in the endodermis regulates mineral movement, while mycorrhizal associations enhance uptake. Phloem loading and unloading processes distribute nutrients throughout the plant.

Mineral Transport Mechanisms

Active and Passive Transport

- Active transport moves minerals against their concentration gradient from areas of low concentration to high concentration
- Requires energy input, typically from ATP hydrolysis
- Allows plants to accumulate essential minerals even when external concentrations are low
- Enables selective uptake of specific minerals
- Passive transport moves minerals down their concentration gradient from areas of high concentration to low concentration
- Does not require energy input
- Includes diffusion and facilitated diffusion through ion channels and carrier proteins
- Occurs when mineral concentrations are higher in the soil solution than in plant cells

Ion Channels and Carrier Proteins

- Ion channels are membrane proteins that form pores allowing specific ions to pass through
- Facilitate rapid passive transport of ions down their electrochemical gradient
- Exhibit selectivity for specific ions based on size and charge (potassium channels)
- Can be gated by voltage, ligands, or mechanical stimuli to regulate ion flow
- Carrier proteins bind to specific minerals and undergo conformational changes to transport them across membranes
- Include both passive transporters (facilitate diffusion) and active transporters (use energy to move against gradient)
- Exhibit high specificity for particular minerals (phosphate transporters)
- Can be regulated by factors such as pH, mineral concentration, and plant signaling molecules

Pathways of Mineral Movement

Symplastic and Apoplastic Pathways

- Symplastic pathway involves mineral movement through the cytoplasm of interconnected cells via plasmodesmata

- Allows minerals to bypass the Casparian strip in the endodermis
- Provides a selective route for mineral transport controlled by the plant
- Requires minerals to cross plasma membranes to enter and exit the symplast
- Apoplastic pathway involves mineral movement through the cell walls and intercellular spaces
- Allows rapid, non-selective transport of minerals in the root cortex
- Restricted by the Casparian strip in the endodermis, which forces minerals into the symplast
- Plays a role in delivering minerals to the xylem for long-distance transport

Casparian Strip

- The Casparian strip is a band of suberin deposited in the radial and transverse cell walls of the endodermis
- Acts as a barrier to the apoplastic movement of water and minerals
- Forces minerals to enter the symplast before reaching the xylem
- Helps maintain root pressure by preventing water loss from the xylem to the soil
- The Casparian strip is not a perfect barrier and some apoplastic bypass flow may occur
- Varies among plant species and environmental conditions
- Can be enhanced by the deposition of additional suberin lamellae in the endodermis (maize under drought stress)

Mineral Uptake Enhancements

Mycorrhizae

- Mycorrhizae are symbiotic associations between plant roots and fungi
- Formed by approximately 80% of land plant species
- Improve plant mineral uptake, particularly phosphorus and nitrogen
- Provide plants with access to a larger soil volume through the extensive fungal mycelium
- Arbuscular mycorrhizae (AM) are the most common type
- Involve fungi from the phylum Glomeromycota
- Form highly branched structures called arbuscules within root cortical cells for nutrient exchange
- Deliver phosphorus directly to the plant via specialized fungal phosphate transporters
- Ectomycorrhizae (EM) are formed by certain tree species with basidiomycete and ascomycete fungi
- Fungal hyphae form a dense sheath around the root and a Hartig net between root cells
- Improve uptake of nitrogen, phosphorus, and other minerals from the soil organic matter
- Provide host plants with protection against pathogens and environmental stresses (drought)

Phloem Transport

Phloem Loading

- Phloem loading is the process of moving sugars and other organic compounds into the phloem for long-distance transport
- Occurs in the source tissues where photosynthates are produced (mature leaves)
- Can be passive (symplastic) or active (apoplastic) depending on the plant species and environmental conditions
- Apoplastic loading involves the use of sucrose-proton symporters to move sugars against their concentration gradient
- Phloem loading is regulated by the activity of enzymes and transporters involved in sugar metabolism and transport
- Sucrose phosphate synthase (SPS) plays a key role in synthesizing sucrose for export
- Sucrose transporters (SUTs) facilitate the uptake of sucrose into companion cells and sieve elements
- Potassium channels and proton pumps establish the osmotic and electrochemical gradients necessary for phloem loading

Phloem Unloading

- Phloem unloading is the process of moving sugars and other organic compounds out of the phloem in sink tissues
- Occurs in the non-photosynthetic tissues that require photosynthates for growth and metabolism (roots, young leaves, fruits)
- Can be symplastic or apoplastic depending on the sink tissue and developmental stage
- Symplastic unloading involves the movement of sugars through plasmodesmata into the recipient cells
- Phloem unloading is influenced by the strength of the sink and the activity of sugar transporters and enzymes
- Invertases hydrolyze sucrose into glucose and fructose, creating a concentration gradient for unloading
- Hexose transporters (HXTs) facilitate the uptake of glucose and fructose into sink cells
- Starch synthases and other enzymes convert the imported sugars into storage compounds (starch in potato tubers)

2.4 Nutrient deficiencies and toxicities

Plants need specific nutrients to thrive, but too much or too little can cause problems. This section explores how nutrient deficiencies and toxicities affect plant growth, showing up as visible symptoms like yellowing leaves or stunted growth.

Understanding these issues is crucial for plant health. We'll learn to spot nutrient problems, their causes, and how to fix them. This knowledge helps us manage plants better and keep them healthy.

Essential Plant Nutrients

Macronutrients and Micronutrients

- Macronutrients are essential elements required by plants in large quantities for proper growth and development (nitrogen, phosphorus, potassium, calcium, magnesium, sulfur)
- Micronutrients are essential elements needed by plants in small quantities but still play crucial roles in various physiological processes (iron, manganese, boron, zinc, copper, molybdenum, chlorine, nickel)
- Both macronutrients and micronutrients are involved in numerous biochemical reactions, including photosynthesis, respiration, and enzyme activation
- Deficiencies in either macronutrients or micronutrients can lead to reduced plant growth, yield, and overall health

Nutrient Mobility in Plants

- Mobile nutrients are elements that can be easily translocated from older leaves to younger leaves or developing tissues when a deficiency occurs (nitrogen, phosphorus, potassium, magnesium)
- Immobile nutrients are elements that cannot be easily translocated within the plant, and deficiency symptoms typically appear in younger leaves first (calcium, iron, boron, copper, manganese)
- Understanding nutrient mobility helps in diagnosing deficiencies based on the location and pattern of symptoms on the plant
- Applying foliar sprays of immobile nutrients can be an effective way to correct deficiencies, as the nutrients are directly absorbed by the leaves

Nutrient Deficiency Symptoms

Visual Indicators of Nutrient Deficiencies

- Chlorosis is the yellowing of leaves due to a lack of chlorophyll, often caused by deficiencies in nitrogen, iron, or magnesium
- Necrosis is the death of plant tissue, which can appear as brown or black spots on leaves, stems, or roots, and can be caused by severe nutrient deficiencies or toxicities
- Other nutrient deficiency symptoms include stunted growth, reduced leaf size, abnormal leaf coloration (purple or red tints), and poor root development
- Regularly monitoring plants for visual symptoms can help identify nutrient deficiencies early, allowing for timely corrective actions

Specific Nutrient Deficiency Symptoms

- Nitrogen deficiency leads to chlorosis in older leaves, as nitrogen is a mobile nutrient, and stunted plant growth
- Phosphorus deficiency causes dark green or purple coloration in older leaves and reduced root growth
- Potassium deficiency results in chlorosis and necrosis along the edges of older leaves and increased susceptibility to diseases

- Calcium deficiency causes necrosis of young leaf tips and poor root development, as calcium is an immobile nutrient
- Iron deficiency leads to interveinal chlorosis in younger leaves, as iron is an immobile nutrient

Nutrient Toxicity and Management

Nutrient Toxicity Symptoms and Causes

- Nutrient toxicity occurs when a plant absorbs excessive amounts of a particular nutrient, leading to adverse effects on plant growth and development
- Toxicity symptoms often resemble nutrient deficiencies, making diagnosis challenging (chlorosis, necrosis, stunted growth)
- Common causes of nutrient toxicities include over-fertilization, poor soil drainage, and low soil pH (which increases the availability of certain nutrients, such as aluminum and manganese)
- Regularly testing soil and plant tissue can help identify potential nutrient toxicities and guide management decisions

Fertilizer Management and Preventing Nutrient Imbalances

- Fertilizers are substances added to the soil to supply essential nutrients and promote plant growth
- Proper fertilizer management involves selecting the appropriate type, rate, and timing of application based on the crop, soil conditions, and growth stage
- Over-application of fertilizers can lead to nutrient toxicities, environmental pollution, and increased production costs
- Implementing best management practices, such as split applications, fertigation, and using slow-release fertilizers, can help prevent nutrient imbalances and optimize nutrient use efficiency
- Regularly monitoring soil and plant nutrient status, along with adjusting fertilizer applications accordingly, is crucial for maintaining optimal plant health and productivity

Unit 3 – Photosynthesis: Light & Carbon Fixation

3.1 Light absorption and photosynthetic pigments

Photosynthetic pigments are the unsung heroes of plant life. Chlorophylls and carotenoids work together to capture light energy, absorbing different wavelengths to maximize efficiency. These pigments are crucial for turning sunlight into usable energy for plants.

Light absorption and energy transfer are the first steps in photosynthesis. Photosystems and light-harvesting complexes team up to capture light and funnel that energy to reaction centers. This process kickstarts the chain of events that ultimately produces food for the plant.

Photosynthetic Pigments

Chlorophylls

- Chlorophyll a is the primary photosynthetic pigment found in all oxygen-evolving photosynthetic organisms
- Chlorophyll a absorbs light most strongly in the blue and red regions of the visible spectrum but poorly in the green region
- Chlorophyll b is an accessory pigment that absorbs light in slightly different regions of the visible spectrum than chlorophyll a, allowing for a broader range of light absorption
- Chlorophyll b transfers the absorbed light energy to chlorophyll a for use in photosynthesis

Carotenoids

- Carotenoids are accessory pigments that absorb light in the blue and green regions of the visible spectrum
- Carotenoids transfer the absorbed light energy to chlorophyll a for use in photosynthesis
- Carotenoids also play a role in photoprotection by dissipating excess light energy as heat, preventing damage to the photosynthetic apparatus (xanthophyll cycle)
- Examples of carotenoids include beta-carotene (orange pigment in carrots) and lutein (yellow pigment in leaves)

Absorption Spectrum

- An absorption spectrum is a graph showing the amount of light absorbed by a pigment at different wavelengths
- Chlorophyll a has absorption peaks in the blue (around 430 nm) and red (around 660 nm) regions of the visible spectrum
- Chlorophyll b and carotenoids have absorption peaks that complement those of chlorophyll a, allowing for a broader range of light absorption

- The absorption spectra of photosynthetic pigments are adapted to the light environment in which the organism lives (aquatic plants absorb different wavelengths than terrestrial plants)

Light Absorption and Energy Transfer

Photosystems

- Photosystems are large protein complexes that contain photosynthetic pigments and are responsible for light absorption and energy transfer
- There are two types of photosystems in oxygenic photosynthesis: Photosystem I (PSI) and Photosystem II (PSII)
- Each photosystem has a reaction center chlorophyll a molecule (P700 in PSI and P680 in PSII) that initiates electron transfer when excited by light
- The reaction center is surrounded by light-harvesting complexes that contain additional chlorophyll and carotenoid molecules

Light-Harvesting Complexes

- Light-harvesting complexes (LHCs) are protein complexes that contain chlorophyll and carotenoid molecules
- LHCs are associated with the photosystems and function to absorb light energy and transfer it to the reaction center
- The arrangement of pigments in LHCs allows for efficient energy transfer through a process called resonance energy transfer
- Examples of LHCs include LHCI (associated with PSI) and LHCII (associated with PSII)

Action Spectrum and Excited State

- An action spectrum is a graph showing the relative effectiveness of different wavelengths of light in driving a photosynthetic process (oxygen evolution or carbon fixation)
- The action spectrum of photosynthesis closely resembles the absorption spectrum of chlorophyll a, indicating that chlorophyll a is the primary pigment driving photosynthesis
- When a pigment molecule absorbs a photon of light, it enters an excited state, where one of its electrons is promoted to a higher energy level
- The excited state is unstable, and the electron quickly returns to its ground state, releasing the absorbed energy as heat, fluorescence, or by transfer to another molecule (photochemistry)

3.2 Electron transport and ATP synthesis

Photosynthesis is all about capturing light energy and turning it into chemical energy. The electron transport chain is the key player here, moving electrons through a series of proteins to create a proton gradient.

This gradient is then used by ATP synthase to make ATP, the energy currency of cells. It's like a molecular waterfall, with protons flowing downhill to power ATP production.

Photosystems and Electron Transport

Light-dependent reactions in photosynthesis

- Photosystems are protein complexes involved in the light-dependent reactions of photosynthesis
- Photosystem II (PSII) and Photosystem I (PSI) work together to capture light energy and convert it into chemical energy
- Light energy is used to excite electrons, which are then transferred through an electron transport chain
- Electron transport chain consists of a series of redox reactions that generate a proton gradient across the thylakoid membrane

Components of the electron transport chain

- Plastoquinone (PQ) is a mobile electron carrier that accepts electrons from PSII and transfers them to the cytochrome b6f complex
- Cytochrome b6f complex is a proton pump that transfers electrons from PQ to plastocyanin while simultaneously pumping protons into the thylakoid lumen
- Plastocyanin (PC) is a mobile electron carrier that accepts electrons from the cytochrome b6f complex and transfers them to PSI
- Ferredoxin (Fd) is an electron acceptor that receives electrons from PSI and transfers them to NADP+ reductase
- NADP+ reductase catalyzes the reduction of NADP+ to NADPH using electrons from ferredoxin (provides reducing power for the Calvin cycle)

Electron flow and energy production

- Light energy excites electrons in PSII, which are then transferred to PSI via the electron transport chain (linear electron flow)
- As electrons flow through the electron transport chain, protons are pumped into the thylakoid lumen, creating a proton gradient
- Proton gradient is used by ATP synthase to generate ATP (chemiosmosis)
- In cyclic electron flow, electrons from PSI are transferred back to the cytochrome b6f complex via ferredoxin, generating ATP without producing NADPH (helps balance ATP and NADPH production)

ATP Synthesis

Proton gradient and chemiosmosis

- Proton gradient is established across the thylakoid membrane during the light-dependent reactions
- Protons accumulate in the thylakoid lumen as a result of water splitting in PSII and proton pumping by the cytochrome b6f complex
- ATP synthase uses the proton gradient to generate ATP through the process of chemiosmosis
- Protons flow down their concentration gradient through ATP synthase, driving the synthesis of ATP from ADP and inorganic phosphate (Pi)

Types of photophosphorylation

- Non-cyclic photophosphorylation involves linear electron flow from PSII to PSI, generating both ATP and NADPH
- Electrons from PSI reduce NADP+ to NADPH, while protons pumped into the thylakoid lumen drive ATP synthesis (produces ATP and NADPH in a ratio of 3:2)
- Cyclic photophosphorylation involves the recycling of electrons from PSI back to the cytochrome b6f complex via ferredoxin
- Cyclic electron flow generates ATP without producing NADPH (helps balance ATP and NADPH production to meet the demands of the Calvin cycle)
- Cyclic photophosphorylation is important under conditions of high ATP demand or low NADPH requirement (such as during photorespiration or nitrogen assimilation)

3.3 Calvin cycle and carbon fixation

The Calvin cycle is the powerhouse of carbon fixation in plants. It's where CO_2 gets transformed into sugar, fueling plant growth. This process happens in the chloroplast stroma, using energy from light reactions to make glucose.

RuBisCO, the star enzyme, kicks off the cycle by fixing carbon. It combines CO_2 with RuBP, creating 3-PGA. This 3-carbon molecule then goes through a series of reactions, using ATP and NADPH from light reactions to eventually form glucose.

Carbon Fixation and Reduction

RuBisCO and Carbon Fixation

- RuBisCO (Ribulose-1,5-bisphosphate carboxylase-oxygenase) is the primary enzyme responsible for carbon fixation, the process of converting atmospheric CO_2 into organic compounds
- It is the most abundant protein on Earth and is found in the chloroplast stroma
- RuBisCO catalyzes the first major step of carbon fixation by combining CO_2 with ribulose 1,5-bisphosphate (RuBP) to form two molecules of 3-phosphoglycerate (3-PGA)
- Carbon fixation occurs during the light-independent reactions of photosynthesis (Calvin cycle) and is crucial for the synthesis of organic compounds
- The process of carbon fixation converts inorganic carbon (CO_2) into organic molecules that can be used by plants for growth and energy storage (glucose, starch)
- Carbon fixation is the primary pathway for the incorporation of carbon into the biosphere and is essential for sustaining life on Earth
- Ribulose 1,5-bisphosphate (RuBP) is a 5-carbon sugar that serves as the initial acceptor molecule for CO_2 during carbon fixation
- RuBP is regenerated at the end of the Calvin cycle to ensure a continuous supply for carbon fixation
- The enzyme phosphoribulokinase catalyzes the phosphorylation of ribulose 5-phosphate to form RuBP, using ATP as the phosphate donor

Products of Carbon Fixation and Their Fate

- 3-Phosphoglycerate (3-PGA) is the immediate product of carbon fixation, formed when RuBisCO adds CO2 to RuBP
- Each molecule of RuBP that undergoes carboxylation produces two molecules of 3-PGA
- 3-PGA is then reduced to form glyceraldehyde 3-phosphate (G3P) using ATP and NADPH generated from the light reactions
- ATP and NADPH, products of the light reactions, are essential for the reduction phase of the Calvin cycle
- ATP provides the energy needed to drive the endergonic reactions of the Calvin cycle, such as the phosphorylation of 3-PGA to form 1,3-bisphosphoglycerate and the regeneration of RuBP
- NADPH serves as the reducing agent, donating electrons to convert 1,3-bisphosphoglycerate into glyceraldehyde 3-phosphate (G3P)
- The use of ATP and NADPH in the Calvin cycle represents the coupling of the light reactions with the light-independent reactions of photosynthesis

Regeneration of RuBP

The Regeneration Phase

- The regeneration phase of the Calvin cycle involves a series of reactions that convert glyceraldehyde 3-phosphate (G3P) back into ribulose 1,5-bisphosphate (RuBP) to maintain the continuous operation of the cycle
- A portion of the G3P produced during the reduction phase is used to regenerate RuBP, while the remaining G3P is used for the synthesis of glucose and other organic compounds
- The regeneration phase involves a complex series of reactions, including isomerization, transketolation, and phosphorylation steps
- Glyceraldehyde 3-phosphate (G3P) is a key intermediate in the regeneration phase of the Calvin cycle
- G3P is a 3-carbon sugar that is produced during the reduction phase of the Calvin cycle by the reduction of 3-PGA
- A portion of the G3P is diverted away from the Calvin cycle to be used for the synthesis of glucose and other organic compounds, while the remaining G3P enters the regeneration phase
- Ribulose 1,5-bisphosphate (RuBP) is regenerated from G3P through a series of reactions in the regeneration phase
- The regeneration of RuBP is essential for the continuous operation of the Calvin cycle, as it ensures a constant supply of the CO2 acceptor molecule
- The enzyme phosphoribulokinase catalyzes the final step of RuBP regeneration, phosphorylating ribulose 5-phosphate using ATP to form RuBP

Energy Requirements for RuBP Regeneration

- ATP is required during the regeneration phase of the Calvin cycle to phosphorylate ribulose 5-phosphate, forming ribulose 1,5-bisphosphate (RuBP)

- The phosphorylation of ribulose 5-phosphate is catalyzed by the enzyme phosphoribulokinase and is an energy-consuming step
- For every three molecules of CO_2 that enter the Calvin cycle, nine molecules of ATP are required for the regeneration of three molecules of RuBP
- The regeneration phase of the Calvin cycle is an energy-demanding process, requiring a significant portion of the ATP generated during the light reactions
- The continuous regeneration of RuBP is essential for maintaining the high efficiency of carbon fixation and the overall productivity of photosynthesis
- The energy requirements for RuBP regeneration highlight the importance of the light reactions in providing the necessary ATP and NADPH for the Calvin cycle to function optimally

3.4 Photorespiration and C4/CAM photosynthesis

Photorespiration is a wasteful process that occurs when Rubisco fixes oxygen instead of carbon dioxide. It reduces photosynthetic efficiency, especially in C3 plants. High temperatures and dry conditions make photorespiration worse, leading to significant carbon loss.

C4 and CAM plants have evolved special mechanisms to concentrate CO_2 around Rubisco. This reduces photorespiration and allows them to thrive in hot, dry environments where C3 plants struggle. These adaptations make photosynthesis more efficient in challenging conditions.

Photorespiration in C3 Plants

The Photorespiration Process

- Photorespiration occurs when Rubisco fixes O_2 instead of CO_2 due to high O_2 concentration or high temperatures
- Leads to the production of 2-phosphoglycolate (2-PG) which is toxic and must be recycled
- 2-PG is converted to glycolate in the chloroplast then transported to peroxisomes and mitochondria for recycling
- Recycling process converts glycolate back into 3-PGA which can re-enter the Calvin cycle
- Photorespiration is an energy-consuming process that reduces the efficiency of photosynthesis (up to 50% of fixed carbon can be lost)

Factors Affecting Photorespiration

- Photorespiration is more prevalent in C3 plants which include most major crops (wheat, rice, soybeans)
- High temperatures increase the rate of photorespiration because Rubisco's affinity for CO_2 decreases while its affinity for O_2 increases
- Dry conditions can cause stomata to close, reducing CO_2 concentration in the leaf and increasing photorespiration
- Photorespiration is less significant in C4 and CAM plants due to their CO_2 concentration mechanisms

C4 Photosynthesis

C4 Plant Anatomy and Physiology

- C4 plants have a unique leaf anatomy known as Kranz anatomy which consists of two distinct photosynthetic cell types: mesophyll cells and bundle sheath cells
- Mesophyll cells form a ring around the bundle sheath cells and contain PEP carboxylase, an enzyme with high affinity for CO_2
- Bundle sheath cells contain Rubisco and carry out the Calvin cycle
- C4 plants have a CO_2 concentration mechanism that allows them to concentrate CO_2 in the bundle sheath cells, reducing photorespiration

The C4 Photosynthetic Pathway

- In mesophyll cells, CO_2 is initially fixed by PEP carboxylase to form a 4-carbon compound (oxaloacetate), hence the name C4 photosynthesis
- The 4-carbon compound is then converted to malate or aspartate and transported to the bundle sheath cells
- In the bundle sheath cells, the 4-carbon compound is decarboxylated, releasing CO_2 which is then fixed by Rubisco in the Calvin cycle
- The remaining 3-carbon compound is transported back to the mesophyll cells to regenerate PEP
- This CO_2 concentration mechanism allows C4 plants to maintain high rates of photosynthesis even in hot, dry conditions (examples: corn, sugarcane, sorghum)

Crassulacean Acid Metabolism (CAM)

CAM Plant Adaptations

- CAM plants are adapted to hot, dry environments and include many succulents (cacti, aloe, jade plant)
- CAM plants have a unique CO_2 concentration mechanism that allows them to open their stomata at night and close them during the day to conserve water
- At night, CAM plants fix CO_2 using PEP carboxylase to form malic acid which is stored in the vacuole
- During the day, the stomata close and the stored malic acid is decarboxylated, releasing CO_2 which is then fixed by Rubisco in the Calvin cycle

The CAM Photosynthetic Pathway

- The CAM pathway is divided into four phases that occur over a 24-hour period
- Phase I (night): Stomata open, CO_2 is fixed by PEP carboxylase to form malic acid which is stored in the vacuole
- Phase II (early morning): Stomata close, malic acid continues to be stored
- Phase III (day): Malic acid is decarboxylated, releasing CO_2 which is fixed by Rubisco in the Calvin cycle

- Phase IV (late afternoon/evening): Malic acid reserves are depleted, stomata may reopen to fix more CO_2 if conditions allow
- The temporal separation of CO_2 fixation and the Calvin cycle in CAM plants allows them to conserve water while still maintaining photosynthesis

Unit 4 – Phloem Transport of Photoassimilates

4.1 Phloem structure and function

Phloem, the plant's sugar highway, moves vital nutrients from leaves to hungry cells. Its structure, with sieve tubes and companion cells, allows for efficient transport. Understanding phloem is key to grasping how plants distribute energy throughout their bodies.

The pressure flow hypothesis explains how phloem sap moves from high to low pressure areas. This process, driven by osmosis, doesn't need extra energy along the way. Phloem's ability to transport sugars is crucial for plant growth and survival.

Phloem Structure

Sieve Elements and Companion Cells

- Sieve elements are the main conducting cells of the phloem
- Lack a nucleus, ribosomes, and a vacuole at maturity to allow for efficient transport of sugars and other organic compounds
- Connected end-to-end to form sieve tubes for long-distance transport
- Companion cells are specialized parenchyma cells that are closely associated with sieve elements
- Contain a nucleus, ribosomes, and other organelles to support the functioning of sieve elements
- Provide energy and assist in loading and unloading of sugars and other compounds into and out of sieve elements (sucrose, amino acids, hormones)

Sieve Plates

- Sieve plates are the end walls of sieve elements that contain numerous pores
- Allow for the passage of phloem sap between adjacent sieve elements
- Pores are lined with callose, a polysaccharide that can regulate the flow of phloem sap by opening or closing the pores (wound response, seasonal changes)
- Sieve plates are an important structural feature that facilitates efficient long-distance transport in the phloem
- Pores are large enough to allow for the passage of macromolecules (proteins, RNA) in addition to sugars and other small organic compounds

Phloem Transport

Pressure Flow Hypothesis

- The pressure flow hypothesis explains the mechanism of phloem transport

- Suggests that the movement of phloem sap is driven by a pressure gradient between the source and sink tissues
- High osmotic potential in the source tissues (leaves) drives the loading of sugars into the phloem, creating a high hydrostatic pressure
- Low osmotic potential in the sink tissues (roots, fruits) leads to the unloading of sugars, creating a low hydrostatic pressure
- The pressure gradient generated by the difference in osmotic potential causes the phloem sap to flow from source to sink
- Flow is passive and does not require energy input along the transport pathway
- Rate of flow is determined by the magnitude of the pressure gradient and the resistance of the phloem pathway (sieve plate pores, viscosity of phloem sap)

Phloem Sap and Translocation

- Phloem sap is the fluid that is transported through the phloem
- Composed primarily of water, sugars (sucrose), amino acids, hormones, and other organic compounds
- Concentrations of solutes in the phloem sap are much higher than in the xylem sap (10-25% vs. <1%)
- Translocation is the long-distance transport of phloem sap from source to sink tissues
- Occurs in both directions, from leaves to roots and from roots to leaves (bidirectional)
- Speed of translocation can range from 1-10 cm/hour, depending on the plant species and environmental conditions (temperature, light intensity)
- Translocation is essential for the distribution of photosynthates and other organic compounds throughout the plant body

Phloem Pathways

Symplastic Pathway

- The symplastic pathway involves the movement of solutes through the cytoplasm of interconnected cells via plasmodesmata
- Plasmodesmata are channels that connect the cytoplasm of adjacent cells, allowing for the direct exchange of small molecules and macromolecules
- Sugars and other organic compounds can move from the mesophyll cells to the phloem through the symplastic pathway (cell-to-cell transport)
- The symplastic pathway is important for the loading of sugars into the phloem in source tissues
- Sugars are actively transported from the mesophyll cells into the companion cells and then into the sieve elements via plasmodesmata
- This process is mediated by sugar transporters and requires energy input (ATP)

Apoplastic Pathway

- The apoplastic pathway involves the movement of solutes through the cell walls and intercellular spaces, outside of the cytoplasm
- Solutes can diffuse freely through the cell walls and intercellular spaces, but must cross the plasma membrane to enter the cytoplasm
- The apoplastic pathway is important for the unloading of sugars from the phloem in sink tissues (roots, fruits)
- The apoplastic pathway is also involved in the retrieval of solutes from the apoplast back into the symplast
- Sugars and other organic compounds that leak out of the phloem can be actively transported back into the phloem via the apoplastic pathway
- This process helps to maintain the pressure gradient and ensures efficient transport of solutes in the phloem

4.2 Sugar loading and unloading mechanisms

Sugar loading and unloading are crucial for plants to move sugars from where they're made to where they're needed. Loading happens in leaves, where sugars enter the phloem through different methods. Unloading occurs in areas that use or store sugars, like fruits and roots.

These processes are key to understanding how plants distribute the energy they make during photosynthesis. By moving sugars around, plants can grow, develop, and respond to their environment. It's like a plant's own delivery system for food and energy.

Sugar Loading Mechanisms

Apoplastic Loading

- Apoplastic loading involves the transport of sugars from the mesophyll cells to the apoplast, the extracellular space surrounding the phloem sieve elements
- Sugars, primarily sucrose, are actively transported across the plasma membrane of companion cells and into the apoplast using proton-coupled sucrose transporters (SUTs)
- The proton gradient required for this active transport is generated by H+-ATPases located on the plasma membrane of companion cells
- Once in the apoplast, sucrose is taken up by the sieve elements through SUTs located on their plasma membrane
- Apoplastic loading is common in many plant species, including important crops such as sugarcane and sugar beet

Symplastic Loading and Polymer Trapping

- Symplastic loading involves the movement of sugars from the mesophyll cells to the phloem sieve elements through plasmodesmata, the cytoplasmic channels connecting adjacent cells
- In some plant species, such as cucurbits (squash and pumpkin), sugars are first converted into larger molecules, such as raffinose and stachyose, through a process called polymer trapping

- These larger sugar molecules are unable to diffuse back through the plasmodesmata, effectively trapping them in the phloem sieve elements
- Polymer trapping maintains a high sugar concentration gradient between the mesophyll cells and the phloem, facilitating continuous symplastic loading
- Symplastic loading and polymer trapping are more energy-efficient compared to apoplastic loading, as they do not require active transport across membranes

Sucrose Transporters and Proton-Coupled Transport

- Sucrose transporters (SUTs) are integral membrane proteins that facilitate the movement of sucrose across cell membranes
- SUTs are involved in both apoplastic and symplastic loading of sugars into the phloem sieve elements
- In apoplastic loading, SUTs use the proton gradient generated by H+-ATPases to actively transport sucrose from the apoplast into the sieve elements
- The proton-sucrose co-transport mechanism allows for the accumulation of sucrose in the phloem against its concentration gradient
- SUTs are also involved in the retrieval of sucrose that may leak out of the phloem during long-distance transport, ensuring efficient sugar delivery to sink tissues
- The expression and activity of SUTs are regulated by various factors, such as plant developmental stage, environmental conditions, and sink demand for sugars

Phloem Unloading and Sink Tissues

Phloem Unloading Mechanisms

- Phloem unloading is the process by which sugars and other organic compounds are released from the phloem sieve elements into the sink tissues
- Unloading can occur through both symplastic and apoplastic pathways, depending on the sink tissue type and developmental stage
- Symplastic unloading involves the movement of sugars through plasmodesmata, directly from the phloem sieve elements into the sink cells
- Apoplastic unloading requires the sugars to be first released into the apoplast and then taken up by the sink cells using sugar transporters
- The unloading mechanism can change during the development of sink tissues, such as in fruits, where a switch from symplastic to apoplastic unloading may occur during ripening

Sink Tissues and Their Roles

- Sink tissues are the sites of sugar utilization and storage in plants, and they rely on the phloem for the supply of organic compounds
- Examples of sink tissues include roots, tubers, developing fruits, seeds, and growing shoots
- Sink tissues can be classified as metabolic sinks or storage sinks, depending on their primary function

- Metabolic sinks, such as root tips and shoot apical meristems, use the imported sugars for growth and development
- Storage sinks, such as tubers (potatoes) and fleshy fruits (tomatoes), accumulate sugars and other organic compounds for later use or as a food source for animals
- The strength of a sink tissue, or its ability to attract sugars, is determined by factors such as the rate of sugar utilization, storage capacity, and the presence of sugar-cleaving enzymes like invertases and sucrose synthases
- The partitioning of sugars between different sink tissues is regulated by the plant's developmental stage, hormonal signals, and environmental factors, ensuring optimal growth and reproduction

4.3 Photoassimilate partitioning and sink-source relationships

Plants distribute their energy resources strategically. Sources like mature leaves produce sugars, while sinks like growing roots and fruits consume them. This balance determines how plants grow and develop.

Sink strength influences which parts get more resources. Strong sinks like fruits compete for limited sugars. This allocation changes as plants grow and respond to their environment, shaping their overall structure and function.

Source-Sink Dynamics

Source and Sink Tissues

- Source tissues are net exporters of carbon assimilates
- Mature leaves are the primary source tissues in plants
- Carry out photosynthesis to produce sugars and other organic compounds
- Export excess assimilates to sink tissues via the phloem
- Sink tissues are net importers of carbon assimilates
- Include growing roots, shoots, developing fruits, and storage organs (tubers, bulbs)
- Depend on imported assimilates from source tissues to sustain growth and development
- Compete for available assimilates based on their sink strength

Sink Strength and Competitive Sinks

- Sink strength refers to the ability of a sink tissue to attract and import assimilates
- Determined by the size, metabolic activity, and developmental stage of the sink
- Sinks with higher sink strength are more competitive and receive a larger share of assimilates
- Examples of strong sinks include rapidly growing fruits, tubers, and meristems
- Competitive sinks vie for limited assimilates exported by source tissues
- Allocation of assimilates among sinks is influenced by their relative sink strengths
- Changes in sink strength during plant development can alter assimilate partitioning patterns
- Environmental factors (temperature, water availability) can also affect sink strength and competition

Assimilate Allocation

Assimilate Partitioning and Phloem Allocation

• Assimilate partitioning refers to the distribution of carbon assimilates among different plant organs

• Determines the relative growth and development of shoots, roots, fruits, and storage organs

• Regulated by source-sink relationships, plant hormones, and environmental factors

• Partitioning patterns can change during different stages of plant growth and development

• Phloem allocation involves the long-distance transport of assimilates from source to sink tissues

• Assimilates are loaded into the phloem in source tissues and unloaded in sink tissues

• Phloem transport is driven by a pressure gradient generated by active loading and unloading processes

• Phloem sap contains sugars, amino acids, hormones, and other organic compounds

Carbon Partitioning

• Carbon partitioning refers to the distribution of carbon among different metabolic pathways and compounds

• Assimilated carbon can be used for growth, respiration, storage, or defense

• Carbon partitioning is influenced by the developmental stage, environmental conditions, and genetic factors

• Example: During fruit development, a larger proportion of carbon is allocated to sugar synthesis and storage

• Carbon partitioning can also be affected by abiotic stresses (drought, nutrient deficiency) and biotic stresses (herbivory, pathogen infection)

Types of Sinks

Metabolic Sinks

• Metabolic sinks are tissues or organs that actively metabolize imported assimilates

• Include actively growing tissues such as shoot and root meristems, expanding leaves, and developing flowers

• Assimilates are used for cell division, cell expansion, and synthesis of structural and functional compounds

• Metabolic sinks have a high demand for energy and carbon skeletons to sustain their growth and development

• Examples of metabolic sinks:

• Apical meristems in shoots and roots

• Expanding leaves and petals

• Developing embryos in seeds

Storage Sinks

• Storage sinks are tissues or organs that accumulate and store assimilates for future use

• Include specialized storage organs such as tubers (potatoes), bulbs (onions), and tap roots (carrots)

• Assimilates are converted into storage compounds such as starch, fructans, or lipids

• Storage sinks act as reservoirs of carbon and energy for plant growth, reproduction, and stress responses

• Examples of storage sinks:

• Potato tubers accumulating starch

• Onion bulbs storing fructans

• Soybean seeds accumulating proteins and lipids

Unit 5 – Respiration and Lipid Metabolism

5.1 Glycolysis and the citric acid cycle

Glycolysis and the citric acid cycle are key players in cellular energy production. They break down glucose and other nutrients, generating ATP and important molecules for various cellular processes.

These pathways work together to extract energy from food. Glycolysis happens in the cell's cytoplasm, while the citric acid cycle occurs in mitochondria. Understanding their steps is crucial for grasping how cells power themselves.

Glycolysis

Overview of Glycolysis

- Glycolysis is a metabolic pathway that breaks down glucose into two pyruvate molecules
- Occurs in the cytoplasm of cells and does not require oxygen (anaerobic)
- Net production of 2 ATP and 2 NADH molecules per glucose molecule
- Consists of two phases: the preparatory phase and the payoff phase
- Key enzymes involved include hexokinase, phosphofructokinase, and pyruvate kinase

Energy and Electron Carriers in Glycolysis

- ATP (adenosine triphosphate) is the primary energy currency of the cell
- Used to drive energy-requiring reactions in glycolysis (phosphorylation of glucose and fructose-6-phosphate)
- Net production of 2 ATP per glucose molecule through substrate-level phosphorylation
- NADH (reduced nicotinamide adenine dinucleotide) is an electron carrier
- Produced during the oxidation of glyceraldehyde-3-phosphate to 1,3-bisphosphoglycerate
- Carries electrons to the electron transport chain for further ATP production

Fate of Pyruvate

- Pyruvate is the end product of glycolysis
- Under aerobic conditions, pyruvate enters the mitochondria for further oxidation in the citric acid cycle
- Under anaerobic conditions, pyruvate can be reduced to lactate (in animals) or ethanol (in yeast and plants)
- Pyruvate is a key metabolic intermediate that links glycolysis to other pathways (citric acid cycle, gluconeogenesis, and amino acid synthesis)

Pyruvate Oxidation

Conversion of Pyruvate to Acetyl-CoA

- Pyruvate is transported into the mitochondrial matrix
- Undergoes oxidative decarboxylation catalyzed by the pyruvate dehydrogenase complex
- Loses a carbon dioxide molecule (decarboxylation) and is oxidized to form acetyl-CoA
- This irreversible reaction links glycolysis to the citric acid cycle

Electron Transfer and NADH Production

- During oxidative decarboxylation, electrons are transferred from pyruvate to NAD+, forming NADH
- NADH carries the electrons to the electron transport chain for ATP production through oxidative phosphorylation
- This step is crucial for generating reducing equivalents (NADH) to drive ATP synthesis

Citric Acid Cycle

Overview of the Citric Acid Cycle

- Also known as the Krebs cycle or tricarboxylic acid (TCA) cycle
- Occurs in the mitochondrial matrix and is a central metabolic hub
- Oxidizes acetyl-CoA derived from carbohydrates, fats, and proteins
- Generates high-energy electron carriers (NADH and $FADH_2$) and GTP (or ATP)
- Produces precursors for amino acid and heme synthesis (α-ketoglutarate, succinyl-CoA)

Acetyl-CoA as the Entry Point

- Acetyl-CoA, produced from pyruvate oxidation, enters the citric acid cycle
- Condenses with oxaloacetate to form citrate, catalyzed by citrate synthase
- This step initiates the cyclic series of reactions in the citric acid cycle
- Acetyl-CoA can also be derived from the breakdown of fatty acids (β-oxidation) and certain amino acids

Energy Production in the Citric Acid Cycle

- The citric acid cycle generates 1 ATP (or GTP) per acetyl-CoA through substrate-level phosphorylation
- Succinyl-CoA synthetase catalyzes the formation of GTP (or ATP) when converting succinyl-CoA to succinate
- The cycle produces 3 NADH and 1 $FADH_2$ per acetyl-CoA
- NADH is generated during the oxidation of isocitrate, α-ketoglutarate, and malate

- $FADH_2$ is produced during the oxidation of succinate to fumarate
- These electron carriers (NADH and $FADH_2$) transfer electrons to the electron transport chain for further ATP production through oxidative phosphorylation

5.2 Electron transport chain and oxidative phosphorylation

The electron transport chain and oxidative phosphorylation are crucial processes in cellular respiration. These mechanisms occur in the inner mitochondrial membrane, where a series of protein complexes transfer electrons and pump protons to create a gradient.

This gradient drives ATP production through ATP synthase, a remarkable enzyme that harnesses the proton flow. Understanding these processes is key to grasping how cells efficiently generate energy from the breakdown of nutrients like glucose and fatty acids.

Electron Transport Chain Components

Structure and Location of the Electron Transport Chain

- Electron transport chain consists of a series of protein complexes and electron carriers embedded in the inner mitochondrial membrane
- Mitochondrial inner membrane houses the electron transport chain components and provides a barrier to maintain the proton gradient necessary for ATP synthesis
- Electron transport chain includes four main protein complexes: NADH dehydrogenase (Complex I), succinate dehydrogenase (Complex II), cytochrome c reductase (Complex III), and cytochrome c oxidase (Complex IV)

Key Components and Their Functions

- NADH dehydrogenase (Complex I) oxidizes NADH, transferring electrons to ubiquinone and pumping protons across the inner mitochondrial membrane
- Ubiquinone (Coenzyme Q10) is a mobile electron carrier that shuttles electrons between NADH dehydrogenase and cytochrome c reductase
- Cytochrome c is a small, soluble protein that transfers electrons from cytochrome c reductase to cytochrome c oxidase
- Cytochrome c oxidase (Complex IV) transfers electrons from cytochrome c to the final electron acceptor, oxygen, while pumping protons across the inner mitochondrial membrane
- Oxygen serves as the final electron acceptor in the electron transport chain, combining with protons to form water

ATP Production

Oxidative Phosphorylation and ATP Synthase

- Oxidative phosphorylation is the process by which ATP is synthesized using the energy from the electron transport chain
- ATP synthase is a large, complex enzyme that catalyzes the synthesis of ATP from ADP and inorganic phosphate (Pi)

- ATP synthase consists of two main components: the F0 subunit, which spans the inner mitochondrial membrane, and the F1 subunit, which protrudes into the mitochondrial matrix
- The F0 subunit acts as a proton channel, allowing protons to flow down their concentration gradient from the intermembrane space to the matrix
- The F1 subunit contains the catalytic sites for ATP synthesis and undergoes conformational changes driven by the proton flow through F0, resulting in ATP production

Proton Gradient and Chemiosmosis

- Proton gradient is established by the pumping of protons from the mitochondrial matrix to the intermembrane space during electron transport
- The accumulation of protons in the intermembrane space creates an electrochemical gradient, with a higher concentration of protons on the outside of the inner mitochondrial membrane
- Chemiosmosis is the process by which the proton gradient is harnessed to drive ATP synthesis
- Protons flow down their concentration gradient through ATP synthase, providing the energy necessary for the conformational changes that lead to ATP production
- The proton gradient is maintained by the continuous pumping of protons by the electron transport chain complexes, ensuring a steady supply of energy for ATP synthesis

5.3 Lipid biosynthesis and degradation

Lipid biosynthesis and degradation are crucial processes in plant metabolism. Plants use fatty acids for energy storage, membrane structure, and signaling. These processes involve complex enzymatic pathways and specialized organelles, allowing plants to efficiently manage their lipid resources.

Fatty acid synthesis occurs in the cytosol, while degradation happens in peroxisomes. Plants can convert lipids to sugars during seed germination. The lipoxygenase pathway modifies fatty acids, producing important signaling molecules for plant defense and communication.

Fatty Acid Synthesis

Acetyl-CoA Carboxylase and Fatty Acid Synthase

- Acetyl-CoA carboxylase catalyzes the first committed step in fatty acid synthesis by converting acetyl-CoA to malonyl-CoA
- Requires biotin as a cofactor and is allosterically regulated by citrate (activator) and palmitoyl-CoA (inhibitor)
- Fatty acid synthase is a multienzyme complex that catalyzes the synthesis of palmitate (16-carbon saturated fatty acid) from acetyl-CoA and malonyl-CoA
- Utilizes NADPH as a reducing agent
- Consists of two identical monomers, each containing multiple enzymatic domains (acyl carrier protein, condensing enzyme, reducing enzymes)
- Fatty acid synthesis occurs in the cytosol of plant cells and is a highly endergonic process requiring significant energy input (ATP and NADPH)

Triacylglycerols and Phospholipids

- Triacylglycerols (triglycerides) are the primary storage form of fatty acids in plant cells
- Consist of three fatty acid molecules esterified to a glycerol backbone
- Stored in specialized organelles called oil bodies or lipid droplets
- Phospholipids are the major structural components of cellular membranes (plasma membrane, organelle membranes)
- Amphipathic molecules with a hydrophilic head (phosphate group and a polar molecule like choline) and hydrophobic tails (fatty acids)
- Arrange into bilayers with hydrophobic tails facing inward and hydrophilic heads facing the aqueous environment
- Both triacylglycerols and phospholipids are synthesized in the endoplasmic reticulum from fatty acids and glycerol-3-phosphate

Fatty Acid Degradation

Beta-oxidation and Lipases

- Beta-oxidation is the primary pathway for fatty acid degradation in plant cells
- Occurs in peroxisomes and glyoxysomes (specialized peroxisomes in germinating seeds)
- Fatty acids are broken down in a cyclic process, removing two carbons at a time as acetyl-CoA
- Acetyl-CoA can enter the citric acid cycle for energy production or be used for gluconeogenesis in germinating seeds
- Lipases are enzymes that catalyze the hydrolysis of ester bonds in lipids, releasing fatty acids and glycerol
- Play a crucial role in mobilizing stored lipids (triacylglycerols) during seed germination and seedling growth
- Also involved in lipid remodeling and signaling processes

Glyoxysomes and Ketone Bodies

- Glyoxysomes are specialized peroxisomes found in germinating seeds of oil-storing plants (castor bean, sunflower)
- Contain enzymes for beta-oxidation and the glyoxylate cycle, which allows the conversion of fatty acids into sugars for seedling growth
- Glyoxylate cycle bypasses the decarboxylation steps of the citric acid cycle, conserving carbon for gluconeogenesis
- Ketone bodies (acetoacetate, beta-hydroxybutyrate) are water-soluble compounds produced from acetyl-CoA when fatty acid breakdown exceeds the capacity of the citric acid cycle
- Can serve as an alternative energy source for tissues during prolonged fasting or stress conditions

- Not as prevalent in plants as in animals, but can accumulate in certain situations (extended darkness, senescence)

Lipid Modification

Lipoxygenase Pathway

- The lipoxygenase pathway is a major route for the oxidative modification of polyunsaturated fatty acids (linoleic acid, linolenic acid) in plants
- Lipoxygenases are non-heme iron-containing enzymes that catalyze the oxygenation of polyunsaturated fatty acids, forming hydroperoxides
- Multiple isoforms exist with different substrate specificities and cellular localizations
- Hydroperoxides can be further metabolized by various enzymes (allene oxide synthase, hydroperoxide lyase) to produce a diverse array of oxylipins
- Oxylipins include jasmonates (jasmonic acid), green leaf volatiles, and divinyl ethers
- The lipoxygenase pathway is involved in various aspects of plant growth, development, and stress responses
- Jasmonates are key signaling molecules in plant defense against herbivores and pathogens
- Green leaf volatiles (hexanal, hexenal) are important in plant-plant communication and plant-insect interactions

Unit 6 – Nitrogen Metabolism and Assimilation

6.1 Nitrogen fixation and symbiotic relationships

Nitrogen fixation is a vital process in plant nutrition, turning atmospheric nitrogen into usable forms. Symbiotic relationships between plants and bacteria, like Rhizobium with legumes, make this possible in nature. These partnerships form specialized root structures called nodules.

Nitrogenase, the key enzyme in this process, needs lots of energy and a low-oxygen environment to work. Plants provide this setup in nodules, along with leghemoglobin to control oxygen levels. In return, bacteria supply plants with fixed nitrogen for growth.

Nitrogen Fixation Process

Converting Atmospheric Nitrogen to Ammonia

• Nitrogen fixation converts atmospheric nitrogen gas (N2) into ammonia (NH3) which can be used by plants

• Occurs through biological nitrogen fixation by bacteria or through industrial processes like the Haber-Bosch process

• Biological nitrogen fixation accounts for about 60% of the total nitrogen fixed on Earth each year

• Crucial step in the nitrogen cycle allows nitrogen to be incorporated into organic compounds and made available to plants and other organisms

Nitrogenase Enzyme and Bacteroids

• Nitrogenase is the enzyme responsible for catalyzing the reduction of atmospheric nitrogen to ammonia

• Consists of two protein components: dinitrogenase reductase (Fe protein) and dinitrogenase (MoFe protein)

• Requires a large amount of energy in the form of ATP (16 ATP per N2 reduced) and a source of electrons (ferredoxin)

• Bacteroids are differentiated bacterial cells within root nodules that contain nitrogenase and carry out nitrogen fixation

• Bacteroids have a larger size, different shape, and altered metabolism compared to free-living bacteria

• Surrounded by a plant-derived membrane called the peribacteroid membrane which controls nutrient exchange

Symbiotic Bacteria

Rhizobium and Legume Symbiosis

• Rhizobium is a genus of gram-negative soil bacteria that forms a symbiotic relationship with legumes

- Infects the roots of leguminous plants, leading to the formation of root nodules
- Within the nodules, Rhizobium differentiates into bacteroids and fixes atmospheric nitrogen for the plant
- In return, the plant provides the bacteria with carbohydrates and a protected environment
- Examples of legumes that form symbiosis with Rhizobium include soybeans, alfalfa, and peas

Frankia and Actinorhizal Symbiosis

- Frankia is a genus of actinobacteria that forms symbiotic relationships with actinorhizal plants
- Actinorhizal plants are a diverse group of woody plants that form root nodules with Frankia, including alders (Alnus), bayberry (Myrica), and sweet fern (Comptonia)
- Frankia infects the roots of actinorhizal plants and induces the formation of root nodules, similar to Rhizobium in legumes
- Within the nodules, Frankia differentiates into vesicles, which are specialized nitrogen-fixing structures

Nod Factors and Symbiosis Establishment

- Nod factors are signaling molecules produced by rhizobia in response to flavonoids secreted by legume roots
- Nod factors are lipochitooligosaccharides (LCOs) that vary in their structure depending on the rhizobial species
- Nod factors trigger a series of responses in the plant root, including root hair curling, infection thread formation, and nodule organogenesis
- Perception of Nod factors by the plant is mediated by LysM receptor-like kinases, which initiate a signaling cascade leading to symbiosis establishment

Plant Structures

Legume Root Nodules

- Legume nodules are specialized plant organs that develop on the roots of leguminous plants in response to infection by rhizobia
- Nodules provide a low-oxygen environment necessary for nitrogenase activity and nitrogen fixation
- Consist of a central zone containing infected plant cells filled with bacteroids, surrounded by uninfected plant cells
- Nodules are connected to the plant's vascular system, allowing for efficient exchange of nutrients between the plant and the bacteria
- Examples of legumes that form nodules include soybeans, peas, and clover

Actinorhizal Root Nodules

- Actinorhizal nodules are formed on the roots of actinorhizal plants in response to infection by Frankia
- Actinorhizal nodules have a coralloid structure, with multiple lobes arising from a common base

- Each lobe contains a central vascular bundle surrounded by cortical cells infected with Frankia
- Actinorhizal nodules have a higher oxygen concentration compared to legume nodules, and Frankia forms specialized vesicles for nitrogen fixation

Leghemoglobin and Oxygen Regulation

- Leghemoglobin is an oxygen-binding protein found in legume nodules, similar to hemoglobin in animal blood
- Produced by the plant in response to rhizobial infection and nodule development
- Leghemoglobin binds to oxygen, maintaining a low oxygen concentration in the nodule to protect nitrogenase from inactivation
- Gives legume nodules their characteristic pink or red color when active
- Oxygen regulation by leghemoglobin is crucial for efficient nitrogen fixation in legume-rhizobia symbiosis

6.2 Nitrate and ammonium assimilation

Nitrate Reduction

Nitrate assimilation is a two-step reduction process that converts nitrate (NO_3^-) all the way down to ammonium (NH_4^+). Each step takes place in a different cellular compartment and uses a different enzyme. Because nitrite is toxic, these steps are tightly coordinated so that intermediates don't accumulate.

Nitrate Reductase Enzyme

Nitrate reductase catalyzes the first step: reduction of nitrate (NO_3^-) to nitrite (NO_2^-). This reaction occurs in the cytosol and requires molybdenum as a cofactor. Electrons for the reduction come from NADH (or NADPH in some species).

This enzyme is the rate-limiting step of nitrate assimilation, so its regulation matters a lot:

- Induced by the presence of nitrate and by light
- Repressed when reduced nitrogen compounds (ammonium, amino acids) accumulate
- Also regulated post-translationally by reversible phosphorylation: phosphorylation in the dark inactivates the enzyme, linking nitrate reduction to photosynthetic activity

Because nitrate reductase controls flux through the whole pathway, its expression level and activity are often used as indicators of a plant's nitrogen assimilation capacity.

Nitrite Reductase Enzyme

Nitrite reductase handles the second step: reduction of nitrite (NO_2^-) to ammonium (NH_4^+). This is a six-electron reduction, and it takes place in the chloroplasts (or plastids in non-photosynthetic tissues).

The electron donor is reduced ferredoxin, which comes directly from the light reactions of photosynthesis. This coupling to the light reactions has two advantages:

- It provides a strong reductant capable of driving the six-electron transfer
- It ensures nitrite reduction is fastest when photosynthesis is active, preventing toxic nitrite buildup

The ammonium produced here feeds directly into the GS-GOGAT cycle for incorporation into amino acids.

Ammonium Assimilation

Whether ammonium arrives from nitrate reduction, photorespiration, or direct root uptake, it needs to be incorporated into organic molecules quickly. Free ammonium is toxic at high concentrations, so plants rely on the GS-GOGAT cycle as their primary assimilation route.

Glutamine Synthetase (GS) Enzyme

Glutamine synthetase catalyzes the ATP-dependent condensation of glutamate and ammonium to form glutamine. This is the entry point for inorganic nitrogen into organic metabolism.

$$\text{Glutamate} + NH_4^+ + ATP \rightarrow \text{Glutamine} + ADP + P_i$$

GS exists as two main isoforms in most plants:

- GS1 (cytosolic): found in roots, phloem, and senescing leaves; important for primary ammonium assimilation in roots and nitrogen remobilization
- GS2 (chloroplastic): dominant in photosynthetic tissues; reassimilates ammonium released during photorespiration

Regulation of GS includes induction by ammonium and light, and feedback inhibition by glutamine and other downstream nitrogen products.

Glutamate Synthase (GOGAT) Enzyme

Glutamate synthase (also called glutamine-2-oxoglutarate aminotransferase, or GOGAT) transfers the amide group of glutamine to 2-oxoglutarate, producing two molecules of glutamate.

$$\text{Glutamine} + \text{2-oxoglutarate} + \text{reductant} \rightarrow \text{2 Glutamate}$$

Two isoforms exist, distinguished by their electron donor:

- Fd-GOGAT (ferredoxin-dependent): predominant in chloroplasts of photosynthetic cells; linked to the light reactions
- NADH-GOGAT: found mainly in non-photosynthetic tissues like roots and developing seeds

GOGAT works in tandem with GS to keep the cycle turning and to regenerate the glutamate substrate that GS needs.

GS-GOGAT Cycle

The GS-GOGAT cycle is the primary pathway for ammonium assimilation in plants. Here's how it works as a cycle:

1. GS combines glutamate + NH_4^+ (using ATP) to produce glutamine
2. GOGAT transfers glutamine's amide group to 2-oxoglutarate, yielding two molecules of glutamate
3. One glutamate recycles back to step 1 as the substrate for GS
4. The other glutamate is available for biosynthesis of other amino acids and nitrogen-containing compounds (nucleotides, chlorophyll, etc.)

The net result of one full turn: one molecule of 2-oxoglutarate and one NH_4^+ are converted into one molecule of glutamate. This cycle is efficient because it keeps ammonium concentrations low (avoiding toxicity) while channeling nitrogen into the amino acid pool.

An older alternative pathway, glutamate dehydrogenase (GDH), can directly combine ammonium with 2-oxoglutarate to form glutamate. However, GDH has a much lower affinity for ammonium than GS, so it plays only a minor role under normal conditions. GDH is thought to function mainly in glutamate catabolism or under stress when ammonium levels spike.

Nitrogen Metabolism

Transamination Reactions

Once glutamate is produced by the GS-GOGAT cycle, the nitrogen it carries needs to be distributed to the full range of amino acids the plant requires. Transamination accomplishes this by transferring an amino group from one amino acid to an α-keto acid, producing a new amino acid and a new keto acid.

These reactions are catalyzed by aminotransferases, which all require the cofactor pyridoxal phosphate (PLP), a derivative of vitamin B_6. Transamination reactions are reversible, which gives plants flexibility to adjust amino acid pools according to metabolic demand.

Two particularly important aminotransferases:

- Aspartate aminotransferase (AAT): converts glutamate + oxaloacetate $\rightleftharpoons$ aspartate + 2-oxoglutarate. This links nitrogen metabolism to the TCA cycle and is critical for aspartate-family amino acid synthesis.
- Alanine aminotransferase (ALT): converts glutamate + pyruvate $\rightleftharpoons$ alanine + 2-oxoglutarate. This becomes especially important under hypoxic conditions (e.g., flooding), when alanine accumulates.

The 2-oxoglutarate released in these reactions can cycle back into the GS-GOGAT pathway, connecting carbon and nitrogen metabolism.

Nitrogen Use Efficiency (NUE)

Nitrogen use efficiency describes how effectively a plant converts available nitrogen into biomass and yield. It's a composite trait with three main components:

- Uptake efficiency: how well roots acquire nitrogen from the soil (influenced by root architecture, transporter expression, and mycorrhizal associations)
- Assimilation efficiency: how effectively acquired nitrogen is incorporated into organic compounds (driven by GS, GOGAT, and related enzymes)
- Remobilization efficiency: how well nitrogen is recycled from senescing or storage tissues to actively growing organs (grain filling, new leaves)

Improving NUE matters because global agriculture applies enormous quantities of nitrogen fertilizer, yet crops typically use only 30-50% of what's applied. The rest is lost to leaching, runoff, and volatilization, causing environmental problems like eutrophication and greenhouse gas emissions.

Current strategies to improve NUE include:

- Overexpression or engineering of key assimilation enzymes (particularly GS and GOGAT isoforms)
- Breeding for deeper or more branched root systems that explore more soil volume

- Precision fertilizer management: matching application rates and timing to actual crop demand and soil nitrogen availability
- Selecting cultivars that remobilize nitrogen efficiently during grain filling

6.3 Amino acid biosynthesis and protein metabolism

Plants are master chemists, creating amino acids from scratch. They use simple molecules like oxaloacetate and α-ketoglutarate to build complex amino acids, grouping them into families based on their origins.

Proteins, the workhorses of cells, are constantly made and broken down. Plants recycle amino acids during senescence, moving nitrogen from old leaves to growing parts. This process is key to efficient nutrient use.

Amino Acid Biosynthesis

Amino Acid Families and Biosynthetic Pathways

- Amino acids are grouped into families based on their biosynthetic pathways and precursor molecules
- Amino acid biosynthesis involves a series of enzymatic reactions that convert precursor molecules into specific amino acids
- The biosynthetic pathways for amino acids are tightly regulated to maintain optimal levels of each amino acid in the cell
- Key enzymes in amino acid biosynthesis are often subject to feedback inhibition by the end product amino acid to prevent excessive accumulation

Aspartate and Glutamate Families

- The aspartate family includes aspartate, asparagine, lysine, methionine, and threonine which are derived from aspartate as a precursor
- Aspartate is synthesized from oxaloacetate, an intermediate of the citric acid cycle, by the enzyme aspartate aminotransferase
- The glutamate family includes glutamate, glutamine, proline, and arginine which are derived from glutamate as a precursor
- Glutamate is synthesized from α-ketoglutarate, an intermediate of the citric acid cycle, by the enzyme glutamate dehydrogenase (using NADPH and NH_4^+)

Aromatic and Branched-Chain Amino Acids

- Aromatic amino acids include phenylalanine, tyrosine, and tryptophan which are derived from the shikimate pathway
- The shikimate pathway begins with the condensation of phosphoenolpyruvate (from glycolysis) and erythrose 4-phosphate (from the pentose phosphate pathway) to form chorismate, the precursor for aromatic amino acids
- Branched-chain amino acids include leucine, isoleucine, and valine which are derived from pyruvate and α-ketobutyrate as precursors
- The biosynthesis of branched-chain amino acids involves a series of parallel reactions catalyzed by enzymes with broad substrate specificity (can act on multiple substrates)

Protein Metabolism

Protein Synthesis and Degradation

- Protein synthesis (translation) occurs on ribosomes and involves the assembly of amino acids into polypeptide chains based on the genetic code
- The process of protein synthesis includes initiation, elongation, and termination steps which are regulated by various factors (initiation factors, elongation factors, release factors)
- Proteolysis is the breakdown of proteins into smaller peptides or individual amino acids by proteolytic enzymes (proteases)
- Proteolysis plays a crucial role in protein turnover, regulation of cellular processes, and recycling of amino acids for new protein synthesis

Nitrogen Remobilization and Senescence

- Nitrogen remobilization involves the redistribution of nitrogen from source tissues (older leaves) to sink tissues (developing leaves, fruits, seeds) during plant growth and development
- During leaf senescence, proteins are degraded and the released amino acids are transported to sink tissues for reuse in new protein synthesis
- Senescence is a highly regulated process that involves the coordinated expression of genes related to protein degradation, nutrient remobilization, and cell death
- Key enzymes involved in nitrogen remobilization during senescence include proteases, glutamine synthetase, and asparagine synthetase which convert amino acids into transportable forms (glutamine, asparagine)

Unit 7 – Plant Hormones: Growth and Signaling

7.1 Classical plant hormones: auxins, cytokinins, gibberellins

Plant hormones are crucial regulators of growth and development. Auxins, cytokinins, and gibberellins are three classical plant hormones that play vital roles in various physiological processes, from cell division to fruit development.

These hormones work together to control plant growth, often with overlapping or antagonistic effects. Understanding their structures, synthesis, and functions is key to grasping how plants respond to environmental cues and internal signals.

Auxins and Their Effects

Auxin Structure and Synthesis

- Auxins are a class of plant hormones that play a crucial role in regulating plant growth and development
- The most common naturally occurring auxin is indole-3-acetic acid (IAA)
- IAA is synthesized primarily in young leaves, shoot tips, and developing seeds
- Tryptophan serves as a precursor for IAA synthesis through multiple biosynthetic pathways
- Auxins can be synthesized in one part of the plant and transported to other regions where they exert their effects
- Auxin transport occurs in a polar manner, with the hormone moving from the shoot apex towards the base of the plant (basipetal transport)

Physiological Effects of Auxins

- Auxins promote apical dominance, the phenomenon where the main central stem of a plant is dominant over other side stems
- Auxins produced by the apical meristem suppress the growth of lateral buds, maintaining a single dominant stem (monopodial growth)
- Removal of the apical meristem (decapitation) reduces auxin levels, allowing lateral buds to grow and branch out (sympodial growth)
- Auxins stimulate cell elongation, particularly in shoots
- They cause cells to take up water and expand, leading to increased plant height
- Auxins induce the expression of genes involved in cell wall loosening (expansins) and cell wall synthesis (cellulose synthase)
- Auxins play a vital role in fruit development
- They stimulate the growth of ovary walls after fertilization, contributing to fruit enlargement

• Auxins also delay fruit ripening and prevent premature fruit drop (abscission)

• Synthetic auxins (2,4-D) are used as herbicides to selectively kill broadleaf weeds by causing uncontrolled growth

Cytokinins and Their Functions

Cytokinin Structure and Synthesis

• Cytokinins are a class of plant hormones that regulate cell division, shoot initiation, and leaf senescence

• The most common naturally occurring cytokinin is zeatin

• Zeatin is synthesized primarily in root tips, young leaves, and developing seeds

• Adenine derivatives serve as precursors for cytokinin synthesis

• Cytokinins can be synthesized in roots and transported to shoots via the xylem

Physiological Effects of Cytokinins

• Cytokinins stimulate cell division (cytokinesis) in plant meristems

• They activate the cell cycle by inducing the expression of cyclin-dependent kinases (CDKs) and cyclins

• Cytokinins maintain the meristematic activity of shoot and root apical meristems

• Cytokinins promote shoot initiation and development

• They stimulate the growth of lateral buds and promote branching

• Cytokinins counteract the apical dominance induced by auxins

• Cytokinins delay leaf senescence (aging)

• They maintain chlorophyll levels and photosynthetic activity in leaves

• Cytokinins upregulate the expression of genes involved in nutrient remobilization and stress responses

Gibberellins and Plant Growth

Gibberellin Structure and Synthesis

• Gibberellins (GAs) are a class of plant hormones that regulate stem elongation, seed germination, and fruit development

• The most biologically active gibberellin is gibberellic acid (GA3)

• GA3 is synthesized in young leaves, root tips, and developing seeds

• The precursor for gibberellin synthesis is geranylgeranyl diphosphate (GGPP)

• Gibberellins can be synthesized in one part of the plant and transported to other regions where they exert their effects

Physiological Effects of Gibberellins

- Gibberellins promote stem elongation
- They stimulate cell division and cell elongation in the intercalary meristem of monocots (grasses)
- Gibberellins induce the expression of genes involved in cell wall loosening (expansins) and cell wall synthesis (xyloglucan endotransglycosylases)
- Gibberellins regulate seed germination
- They break seed dormancy by promoting the synthesis of hydrolytic enzymes (α-amylase) that mobilize stored reserves
- Gibberellins counteract the effects of abscisic acid (ABA), a hormone that maintains seed dormancy
- Gibberellins influence fruit development
- They stimulate fruit growth and enlargement
- Gibberellins delay fruit ripening and prevent premature fruit drop (abscission)
- Gibberellin mutants exhibit dwarfism (reduced stem elongation) and delayed flowering

7.2 Ethylene, abscisic acid, and brassinosteroids

Plant hormones are crucial for growth and development. Ethylene, abscisic acid, and brassinosteroids play key roles in various processes. These hormones regulate everything from fruit ripening to stress responses, shaping how plants adapt to their environment.

Understanding these hormones is essential for grasping plant physiology. They influence seedling development, stomatal regulation, and cell elongation. Their interactions and signaling pathways are complex, but vital for plant survival and productivity in changing conditions.

Ethylene and Plant Development

Ethylene's Role in Plant Growth and Development

- Ethylene, a gaseous plant hormone, plays a crucial role in various aspects of plant growth and development
- Produced by almost all parts of higher plants, including leaves, stems, roots, flowers, fruits, tubers, and seeds
- Ethylene biosynthesis increases during fruit ripening, flower senescence, leaf abscission, and in response to various stresses (mechanical wounding, flooding, chilling, disease)
- Acts at very low concentrations in the plant (less than 1 ppm)
- Ethylene perception involves a family of membrane-associated receptors (ETR1, ETR2, ERS1, ERS2, EIN4) that bind ethylene and initiate signal transduction

Triple Response and Seedling Development

- Triple response, a characteristic set of morphological changes in etiolated seedlings exposed to ethylene, includes inhibition of stem elongation, radial swelling of the stem, and horizontal growth of the seedling

- Observed in dicotyledonous seedlings (pea, bean, Arabidopsis) and some monocotyledonous seedlings (rice, wheat)
- Used as a bioassay to screen for ethylene-insensitive mutants and to study the ethylene signaling pathway
- Ethylene promotes the formation of root hairs and adventitious roots, which enhance nutrient and water uptake in seedlings
- Inhibits root and shoot elongation, allowing seedlings to redirect resources towards stress adaptation

Fruit Ripening and Senescence

- Ethylene is known as the "ripening hormone" due to its critical role in the ripening process of climacteric fruits (tomato, banana, apple, avocado)
- Stimulates the expression of genes involved in cell wall softening, color change (chlorophyll degradation and carotenoid accumulation), and aroma development
- Autocatalytic ethylene production occurs during fruit ripening, where ethylene promotes its own synthesis, leading to a rapid increase in ethylene levels
- Ethylene induces the senescence of leaves, flowers, and fruits, characterized by chlorophyll breakdown, nutrient remobilization, and organ abscission
- Exogenous application of ethylene can accelerate senescence (cut flowers), while ethylene inhibitors (1-MCP) can delay senescence and extend shelf life

Abscisic Acid (ABA) Functions

Stomatal Regulation and Water Conservation

- Abscisic acid (ABA), a sesquiterpenoid hormone, regulates various aspects of plant growth and development, particularly in response to abiotic stresses
- Plays a key role in stomatal closure during water deficit conditions, reducing transpirational water loss and maintaining plant water balance
- ABA accumulates in guard cells during drought stress, triggering the efflux of potassium ions and the loss of turgor pressure, leading to stomatal closure
- ABA-mediated stomatal regulation involves the activation of guard cell anion channels (SLAC1) and the inhibition of plasma membrane H+-ATPases
- Exogenous application of ABA can induce stomatal closure and enhance drought tolerance in plants (wheat, maize, tomato)

Seed Dormancy and Germination Control

- ABA is a central regulator of seed dormancy, preventing premature germination and ensuring seed survival under unfavorable conditions
- High ABA levels in mature seeds maintain dormancy by inhibiting germination-related processes (embryo growth, reserve mobilization, radicle protrusion)
- ABA biosynthesis and catabolism are tightly regulated during seed development and germination, with ABA levels declining during imbibition to allow germination to proceed

• ABA-deficient mutants (aba1, aba2, aba3) exhibit reduced seed dormancy and precocious germination, while ABA-insensitive mutants (abi3, abi4, abi5) show altered seed maturation and storage reserve accumulation

• Exogenous ABA application can induce secondary dormancy in non-dormant seeds, while ABA biosynthesis inhibitors (fluridone) can promote germination

Abiotic Stress Response and Adaptation

• ABA is a key mediator of plant responses to various abiotic stresses, including drought, salinity, and cold

• Accumulates in plant tissues during stress conditions, triggering a cascade of adaptive responses at the molecular, cellular, and physiological levels

• Induces the expression of stress-responsive genes (LEA proteins, dehydrins, osmolytes) that confer stress tolerance and protect cellular structures from damage

• Promotes root growth and root system architecture remodeling to enhance water and nutrient uptake under stress conditions

• ABA-mediated stress signaling involves the activation of SnRK2 protein kinases and the regulation of transcription factors (ABFs, AREBs) that control stress-responsive gene expression

Brassinosteroids

Brassinosteroid Structure and Biosynthesis

• Brassinosteroids, a class of polyhydroxylated steroid hormones, are essential for various aspects of plant growth and development

• Structurally similar to animal steroid hormones (testosterone, estradiol) but with distinct functions in plants

• Brassinolide, the most bioactive brassinosteroid, was first isolated from Brassica napus (rapeseed) pollen

• Brassinosteroid biosynthesis occurs via the mevalonate pathway and involves a series of oxidation and reduction steps catalyzed by cytochrome P450 enzymes (DWF4, CPD, ROT3)

• Brassinosteroid-deficient mutants (dwf1, dwf4, cpd) exhibit dwarfism, reduced fertility, and altered leaf morphology, highlighting the importance of brassinosteroids in plant development

Cell Elongation and Plant Growth Regulation

• Brassinosteroids promote cell elongation and expansion, particularly in young tissues (hypocotyls, petioles, leaves)

• Stimulate cell wall loosening by inducing the expression of cell wall-modifying enzymes (expansins, xyloglucan endotransglycosylases)

• Interact with other plant hormones (auxins, gibberellins) to regulate cell elongation and plant growth

• Exogenous application of brassinosteroids can increase plant height, leaf size, and biomass accumulation in various crop species (rice, tomato, soybean)

- Brassinosteroid-insensitive mutants (bri1, bin2) exhibit reduced cell elongation and compact plant architecture

Stress Tolerance and Defense Responses

- Brassinosteroids enhance plant tolerance to a wide range of abiotic stresses, including drought, salinity, extreme temperatures, and heavy metals
- Modulate the expression of stress-responsive genes and the accumulation of protective compounds (proline, glycine betaine, polyamines)
- Interact with other stress hormones (ABA, ethylene) to fine-tune plant responses to environmental challenges
- Brassinosteroids also participate in plant defense against biotic stresses, such as pathogen infection and insect herbivory
- Enhance the accumulation of defense-related compounds (phytoalexins, glucosinolates) and the activation of defense signaling pathways (salicylic acid, jasmonic acid)

7.3 Hormone signal transduction and cross-talk

Plant hormones are chemical messengers that regulate growth and development. Their effects depend on complex signal transduction pathways, which convert hormone signals into cellular responses. These pathways involve receptor proteins, second messengers, and transcription factors that amplify and relay the signal.

Hormones don't act in isolation but interact through cross-talk mechanisms. This allows for synergistic or antagonistic effects between different hormones. Maintaining the right hormone balance is crucial for normal plant growth and can be manipulated for agricultural purposes.

Hormone Signal Transduction

Signal Transduction Pathways and Receptor Proteins

- Signal transduction pathways convert extracellular signals into intracellular responses
- Pathways involve a series of molecular interactions and modifications
- Receptor proteins bind to specific hormones and initiate signal transduction
- Receptors can be located on the cell surface or within the cell
- Binding of hormone to receptor causes conformational changes that activate the receptor
- Types of receptor proteins include G protein-coupled receptors (GPCRs) and receptor kinases
- GPCRs are associated with G proteins that activate downstream signaling cascades (auxin and gibberellin receptors)
- Receptor kinases have enzymatic activity and can directly phosphorylate target proteins (ethylene and cytokinin receptors)

Second Messengers and Transcription Factors

- Second messengers are small molecules that relay signals from receptors to target molecules

- Examples include cyclic AMP (cAMP), calcium ions (Ca2+), and inositol trisphosphate (IP3)
- Second messengers amplify the initial signal and activate various cellular responses
- Transcription factors are proteins that regulate gene expression in response to hormone signals
- Activated transcription factors bind to specific DNA sequences and promote or repress transcription
- Examples include auxin response factors (ARFs) and ethylene-insensitive 3 (EIN3)
- Transcriptional regulation by hormones leads to changes in protein synthesis and cellular activity

Signal Amplification

- Signal amplification occurs at multiple steps in the transduction pathway
- Amplification allows a small number of hormone molecules to generate a large cellular response
- Mechanisms of amplification include enzyme activation cascades and positive feedback loops
- Enzyme activation cascades involve sequential activation of multiple enzymes, each amplifying the signal
- Positive feedback loops occur when a signaling molecule enhances its own production or activity
- Signal amplification ensures that hormone signals are efficiently transmitted and elicit appropriate physiological responses

Hormone Interactions

Hormone Cross-talk

- Hormone cross-talk refers to the interactions between different hormone signaling pathways
- Cross-talk allows for integration and coordination of multiple hormone responses
- Mechanisms of cross-talk include shared signaling components and regulation of hormone biosynthesis or degradation
- Shared signaling components, such as transcription factors, can be activated by multiple hormones (EIN3 in ethylene and jasmonic acid signaling)
- One hormone can influence the biosynthesis or degradation of another hormone (auxin promotes ethylene biosynthesis)
- Cross-talk enables fine-tuning of plant responses to environmental and developmental cues

Synergistic and Antagonistic Effects

- Synergistic effects occur when the combined action of two or more hormones is greater than the sum of their individual effects
- Example: auxin and cytokinin synergistically promote cell division in tissue culture
- Synergism can result from positive cross-talk between signaling pathways
- Antagonistic effects occur when one hormone opposes or inhibits the action of another hormone
- Example: abscisic acid (ABA) antagonizes the growth-promoting effects of gibberellins

- Antagonism can result from negative cross-talk or competition for shared signaling components
- Synergistic and antagonistic interactions contribute to the complex regulation of plant growth and development

Hormone Balance

- Hormone balance refers to the relative levels and ratios of different hormones in plant tissues
- Optimal hormone balance is crucial for normal plant growth and development
- Hormone balance is maintained through regulated biosynthesis, transport, and degradation
- Biosynthesis and degradation rates are modulated in response to environmental and developmental signals
- Transport mechanisms ensure proper distribution of hormones throughout the plant
- Alterations in hormone balance can lead to abnormal growth patterns and physiological responses (dwarf or elongated phenotypes)
- Understanding hormone balance is essential for manipulating plant growth in agriculture and horticulture (applying plant growth regulators)

7.4 Novel plant growth regulators and their functions

Plant growth regulators are crucial for plant development and defense. Jasmonates and salicylic acid play key roles in protecting plants from pests and pathogens. These hormones trigger defense responses and help plants fine-tune their reactions to different threats.

Strigolactones and polyamines are emerging as important plant growth regulators. Strigolactones control branching and root development, while polyamines influence cell division and stress responses. Peptide hormones also regulate various aspects of plant growth and development.

Plant Defense Signaling

Jasmonates and Salicylic Acid in Plant Defense

- Jasmonates are lipid-derived hormones that play a crucial role in plant defense against herbivores and necrotrophic pathogens
- Jasmonic acid (JA) is the most well-known jasmonate involved in defense signaling
- JA accumulates in response to wounding, herbivory, or pathogen attack, triggering the expression of defense-related genes (proteinase inhibitors, defensins)
- Salicylic acid (SA) is a phenolic compound that plays a central role in plant defense against biotrophic pathogens
- SA levels increase upon pathogen infection, leading to the activation of defense responses (pathogenesis-related proteins, cell wall reinforcement)
- SA and JA signaling pathways often exhibit antagonistic interactions, allowing plants to fine-tune their defense responses based on the type of attacker

Systemic Acquired Resistance and Defense Signaling

- Systemic acquired resistance (SAR) is a long-lasting, broad-spectrum defense response that occurs in distal parts of the plant following a localized infection
- SAR is mediated by SA and involves the systemic accumulation of PR proteins, enhancing resistance to subsequent pathogen attacks
- Mobile signals, such as methyl salicylate (MeSA) and azelaic acid, are proposed to be involved in the long-distance transmission of SAR
- Defense signaling in plants involves a complex network of hormones, reactive oxygen species (ROS), and calcium signaling
- ROS, such as hydrogen peroxide (H2O2), act as signaling molecules in defense responses, triggering cell wall reinforcement and HR
- Calcium influx and calcium-dependent protein kinases (CDPKs) play a crucial role in transducing defense signals and activating downstream responses (transcription factors, defense gene expression)

Plant Growth and Development Regulators

Strigolactones and Branching Inhibition

- Strigolactones are carotenoid-derived hormones that regulate plant architecture and development
- Strigolactones are synthesized in roots and transported to shoots, where they inhibit axillary bud outgrowth and branching
- Strigolactone biosynthesis involves carotenoid cleavage dioxygenases (CCDs) and cytochrome P450 enzymes (MAX1)
- Strigolactone signaling is mediated by the F-box protein MAX2 and the α/β hydrolase D14, which form a complex to degrade transcriptional repressors (SMXLs) and promote branching inhibition
- Strigolactones also play a role in root development, leaf senescence, and symbiotic interactions with arbuscular mycorrhizal fungi

Polyamines and Peptide Hormones in Growth and Development

- Polyamines, such as putrescine, spermidine, and spermine, are small aliphatic amines that regulate various aspects of plant growth and development
- Polyamines are involved in cell division, embryogenesis, fruit ripening, and abiotic stress responses (drought, salinity)
- Polyamine biosynthesis involves the decarboxylation of amino acids (arginine, ornithine) and the sequential addition of aminopropyl groups by spermidine and spermine synthases
- Peptide hormones are small signaling molecules that regulate various developmental processes in plants
- Examples of peptide hormones include systemins (wound response), CLAVATA3 (meristem maintenance), and RALF (rapid alkalinization factor) peptides
- Peptide hormones are perceived by receptor-like kinases (RLKs) at the plasma membrane, initiating signaling cascades that modulate gene expression and cellular responses

Unit 8 – Plant Development: Seed to Senescence

8.1 Seed germination and seedling growth

Seed germination marks the start of a plant's life cycle, transforming dormant seeds into vibrant seedlings. This process involves complex physiological changes, from water uptake to enzyme activation, setting the stage for growth.

As seedlings emerge, they face critical developmental decisions. Light exposure triggers photomorphogenesis, while darkness leads to skotomorphogenesis. Plant hormones like gibberellins and abscisic acid play key roles in regulating these early growth stages.

Seed Germination Stages

Dormancy and Imbibition

- Seeds remain dormant until favorable conditions for germination are met (adequate moisture, temperature, oxygen)
- Seed coat protects the embryo during dormancy and prevents premature germination
- Imbibition is the uptake of water by the dry seed which activates metabolic processes
- Water uptake causes the seed to swell and soften, allowing enzymes to become active
- Respiration rate increases as the seed hydrates providing energy for growth

Radicle Emergence and Cotyledon Development

- The radicle (embryonic root) is the first structure to emerge from the seed during germination
- Radicle grows downward in response to gravity (gravitropism) to establish the root system
- Cotyledons are the embryonic leaves that store food reserves (starch, proteins, lipids) in many seeds
- Cotyledons may remain below ground (hypogeal germination) or emerge above ground (epigeal germination)
- In epigeal germination, cotyledons become photosynthetic and provide nutrients until true leaves develop (beans, lettuce)
- In hypogeal germination, cotyledons remain below ground and the epicotyl emerges (peas, corn)

Seedling Growth and Development

Hypocotyl and Epicotyl Growth

- The hypocotyl is the stem region below the cotyledons that elongates during germination
- Hypocotyl growth pushes the cotyledons and shoot tip above the soil surface in epigeal germination
- The epicotyl is the stem region above the cotyledons that gives rise to the first true leaves

- Epicotyl growth occurs after the cotyledons have emerged or the shoot tip has been pushed above the soil

Photomorphogenesis and Skotomorphogenesis

- Photomorphogenesis is the development of the seedling in the presence of light
- Light triggers the opening of the apical hook, expansion of the cotyledons, and greening of the seedling (chlorophyll synthesis)
- Photomorphogenesis is mediated by phytochromes (red/far-red light receptors) and cryptochromes (blue light receptors)
- Skotomorphogenesis (etiolation) is the development of the seedling in the absence of light
- Seedlings have elongated hypocotyls, closed cotyledons, and underdeveloped chloroplasts (appear pale yellow)
- Skotomorphogenesis allows the seedling to rapidly grow towards the soil surface to access light

Plant Hormones in Germination and Growth

Gibberellins Promote Germination and Seedling Growth

- Gibberellins (GA) are plant hormones that stimulate seed germination and seedling growth
- GA is synthesized in the embryo and released during imbibition
- GA activates enzymes (alpha-amylase) that break down stored starch in the endosperm to provide energy for growth
- GA promotes stem and leaf growth by stimulating cell division and elongation
- Dwarf mutants (corn, peas) are deficient in GA synthesis or signaling resulting in reduced stem growth

Abscisic Acid Maintains Dormancy and Inhibits Growth

- Abscisic acid (ABA) is a plant hormone that maintains seed dormancy and inhibits germination
- ABA levels are high in dormant seeds and decrease during imbibition allowing germination to proceed
- ABA inhibits GA synthesis and activity in the seed preventing premature germination
- ABA is involved in stress responses (drought, salinity) and promotes stomatal closure to reduce water loss
- Exogenous application of ABA can be used to prolong seed storage and improve stress tolerance in crops

8.2 Vegetative growth and organogenesis

Plant development is a fascinating journey from seed to maturity. Vegetative growth and organogenesis are key processes that shape a plant's structure. These processes involve the activity of meristems, specialized regions of dividing cells that drive growth and form new organs.

Meristems are the architects of plant development, creating leaves, roots, and stems. Understanding how meristems work and how they're regulated by hormones and environmental factors is crucial for grasping plant growth patterns and overall structure.

Meristems and Plant Development

Apical Meristems and Cell Differentiation

- Located at the tips of shoots and roots, apical meristems are regions of actively dividing cells responsible for primary growth and elongation
- Apical meristems give rise to three primary meristems: protoderm (develops into epidermis), ground meristem (develops into ground tissue), and procambium (develops into vascular tissue)
- Cell differentiation is the process by which meristematic cells specialize and develop into specific cell types with distinct functions
- Differentiation is influenced by various factors, including plant hormones (auxins and cytokinins), gene expression, and environmental cues

Leaf and Root Development

- Leaf development (phyllotaxy) is initiated by the shoot apical meristem (SAM) and involves the formation of leaf primordia, which develop into mature leaves
- Leaf primordia arise from the peripheral zone of the SAM in a specific pattern (spiral, alternate, opposite, or whorled) determined by genetic and environmental factors
- Root development originates from the root apical meristem (RAM) located at the tip of the root
- The RAM is protected by the root cap and gives rise to the root epidermis, cortex, and vascular tissue
- Lateral roots form from the pericycle, a layer of cells adjacent to the vascular tissue in the root

Stem Elongation and Lateral Meristems

- Stem elongation occurs through the activity of the shoot apical meristem and the elongation of internodes (regions between leaf nodes)
- Lateral meristems, including the vascular cambium and cork cambium, are responsible for secondary growth (increase in girth) of stems and roots
- The vascular cambium produces secondary xylem (wood) and secondary phloem (inner bark), leading to the thickening of stems and roots in woody plants
- The cork cambium (phellogen) produces the periderm, a protective outer layer that replaces the epidermis in woody plants, consisting of the phellogen, phellem (cork), and phelloderm

Phyllotaxy and Branching

Phyllotaxy and Shoot Branching

- Phyllotaxy refers to the arrangement of leaves on a stem, which can be spiral (alternate), opposite, or whorled
- The divergence angle between successive leaves in a spiral phyllotaxy is often close to the golden angle (137.5°), optimizing light interception and minimizing shading
- Shoot branching involves the formation of axillary buds in the axils of leaves, which can develop into lateral branches

- Apical dominance, the suppression of axillary bud growth by the shoot apex, is regulated by plant hormones (auxins and cytokinins)

Auxins and Cytokinins in Branching

- Auxins, produced in the shoot apex and young leaves, are transported basipetally (downward) and inhibit the growth of axillary buds, maintaining apical dominance
- Removal of the shoot apex (decapitation) or damage to the plant can reduce auxin levels and promote the growth of axillary buds, leading to branching
- Cytokinins, produced in roots and transported acropetally (upward), promote cell division and stimulate the growth of axillary buds
- The balance between auxins and cytokinins plays a crucial role in regulating shoot branching and plant architecture
- Environmental factors, such as light intensity and quality, can also influence branching patterns by altering hormone levels and signaling pathways (shade avoidance response)

8.3 Flowering and reproductive development

Flowering and reproductive development are crucial stages in a plant's life cycle. This process involves complex interactions between environmental cues, internal signals, and genetic factors that regulate the transition from vegetative to reproductive growth.

Floral induction, development, and reproduction involve intricate mechanisms. From photoperiodic control and vernalization to the formation of gametes and fertilization, these processes ensure successful reproduction and adaptation to diverse environments.

Floral Induction

Photoperiodic Control of Flowering

- Photoperiodism is the physiological response of organisms to the length of day or night
- Plants can be classified as long-day plants (flower when the day exceeds a critical length), short-day plants (flower when the day is less than a critical length), or day-neutral plants (flower regardless of day length)
- Phytochromes (light-sensitive proteins) play a crucial role in detecting day length and regulating flowering time
- The circadian clock, an internal timekeeping mechanism, interacts with phytochromes to measure day length and control flowering (Arabidopsis thaliana)

Vernalization and Temperature Effects on Flowering

- Vernalization is the process by which prolonged exposure to cold temperatures promotes flowering in certain plants
- Cold exposure induces epigenetic changes (modifications to DNA without altering the sequence) that regulate flowering time genes (winter wheat, biennial beets)
- Vernalization ensures that plants flower in the appropriate season, avoiding damage from cold temperatures

- Some plants also respond to warm temperatures, which can either promote or delay flowering depending on the species (pea, Arabidopsis)

Florigen: The Elusive Flowering Hormone

- Florigen is a hypothetical hormone that is produced in leaves under favorable conditions and transported to the shoot apical meristem to induce flowering
- The identity of florigen remained elusive for decades, but recent research suggests that it may be a small protein called FT (Flowering Locus T) in Arabidopsis
- FT protein is produced in leaves and transported through the phloem to the shoot apical meristem, where it interacts with other proteins to initiate flowering
- The discovery of florigen has provided insights into the long-distance signaling mechanisms that regulate flowering in plants (rice, tomato)

Floral Development

Floral Meristem Identity and Floral Organ Formation

- Floral meristem identity genes, such as LEAFY and APETALA1 in Arabidopsis, are responsible for converting the shoot apical meristem into a floral meristem
- Once the floral meristem is established, floral organ identity genes control the development of sepals, petals, stamens, and carpels
- Floral organ identity genes are classified into four classes (A, B, C, and E) based on their functions and interactions
- Mutations in floral organ identity genes can lead to homeotic transformations, where one organ type develops in place of another (Arabidopsis, snapdragon)

The ABCE Model of Floral Organ Identity

- The ABCE model explains how the combinatorial action of floral organ identity genes determines the formation of floral organs
- Class A genes (APETALA1 and APETALA2 in Arabidopsis) specify sepal and petal identity
- Class B genes (APETALA3 and PISTILLATA in Arabidopsis) specify petal and stamen identity
- Class C genes (AGAMOUS in Arabidopsis) specify stamen and carpel identity
- Class E genes (SEPALLATA1-4 in Arabidopsis) are required for the function of A, B, and C genes and the formation of all floral organs

Inflorescence Architecture and Diversity

- An inflorescence is a group of flowers arranged on a stem according to a specific pattern
- Inflorescences can be classified as determinate (flowers are produced in a defined sequence and the apical meristem eventually forms a terminal flower) or indeterminate (flowers are produced continuously and the apical meristem remains active)
- The arrangement of flowers within an inflorescence is controlled by genes that regulate meristem identity and branching patterns (tomato, maize)

- Inflorescence architecture varies widely among plant species and can affect pollination, fruit set, and yield (grapes, sunflower)

Reproductive Processes

Gametogenesis: Formation of Male and Female Gametes

- Gametogenesis is the process by which diploid cells undergo meiosis to produce haploid gametes (sperm and egg cells)
- In angiosperms, male gametogenesis occurs in the anthers and involves the formation of pollen grains containing sperm cells
- Female gametogenesis occurs in the ovules and involves the formation of an embryo sac containing the egg cell and other supportive cells
- Gametogenesis ensures the production of genetically diverse gametes and is a critical step in sexual reproduction (lily, maize)

Pollination: Transfer of Pollen from Anther to Stigma

- Pollination is the transfer of pollen grains from the anther of a stamen to the stigma of a carpel
- Pollination can be mediated by various agents, such as wind, water, insects, birds, or mammals, depending on the plant species
- Flowers have evolved various adaptations to attract pollinators, such as colorful petals, scent, and nectar rewards (orchids, snapdragons)
- Successful pollination is essential for fertilization and seed set, and many crops rely on animal pollinators for yield (almonds, apples)

Fertilization: Fusion of Gametes and Seed Development

- Fertilization is the fusion of male and female gametes to form a zygote, which develops into an embryo
- In angiosperms, double fertilization occurs, where one sperm cell fuses with the egg cell to form the zygote, and another sperm cell fuses with two polar nuclei to form the endosperm (a nutritive tissue)
- After fertilization, the ovule develops into a seed, which contains the embryo, endosperm, and protective seed coat
- Seed development involves the coordinated growth and differentiation of the embryo and endosperm, as well as the accumulation of storage reserves (starch, proteins, oils) that support germination and seedling growth (beans, corn)

8.4 Fruit ripening and senescence

Fruit ripening and senescence are crucial stages in a plant's life cycle. These processes involve complex hormonal and physiological changes that transform fruits and prepare plants for seasonal transitions.

From ethylene-driven ripening to programmed cell death, plants undergo remarkable transformations. Understanding these processes helps us grasp how plants adapt, conserve resources, and prepare for new growth cycles.

Fruit Ripening

Types of Fruit Ripening

- Climacteric fruits exhibit a burst of ethylene production and a peak in cellular respiration at the onset of ripening (tomatoes, bananas, apples)
- Non-climacteric fruits do not show a dramatic change in ethylene production or respiration rate during ripening (citrus fruits, grapes, strawberries)
- Ethylene, a gaseous plant hormone, plays a crucial role in regulating the ripening process in climacteric fruits
- Ethylene binds to receptors and initiates a signaling cascade that leads to changes in gene expression and fruit ripening
- Exogenous application of ethylene can accelerate ripening in climacteric fruits

Physiological Changes During Fruit Ripening

- Fruit softening occurs due to the breakdown of cell wall components, such as pectin and hemicellulose, by enzymes (polygalacturonase, pectin methylesterase)
- Softening makes fruits more palatable and easier to eat
- Excessive softening can lead to fruit spoilage and reduced shelf life
- Pigment changes during ripening involve the degradation of chlorophyll and the synthesis of other pigments (carotenoids, anthocyanins)
- Chlorophyll degradation leads to the loss of green color
- Carotenoids impart yellow and orange colors to fruits (oranges, mangoes)
- Anthocyanins are responsible for red, purple, and blue colors in fruits (blueberries, grapes)

Senescence and Abscission

Programmed Cell Death and Leaf Senescence

- Senescence is a genetically programmed process leading to the death of cells, tissues, or organs
- Programmed cell death (PCD) is a controlled process that eliminates damaged or unwanted cells
- PCD occurs during leaf senescence, allowing plants to remobilize nutrients to other parts of the plant
- Leaf senescence is characterized by the degradation of chlorophyll, proteins, and other macromolecules
- Environmental factors (drought, nutrient deficiency) and internal signals (age, hormones) can trigger leaf senescence

Abscission and Nutrient Remobilization

- Abscission is the controlled separation of leaves, flowers, or fruits from the plant
- Abscission occurs at specialized cell layers called abscission zones

• Enzymes (cellulases, polygalacturonases) degrade the cell walls in the abscission zone, allowing the organ to detach

• Nutrient remobilization is the process by which plants redistribute nutrients from senescing tissues to developing parts of the plant

• During leaf senescence, nutrients (nitrogen, phosphorus) are transported from the leaves to the stem, roots, or developing fruits and seeds

• Efficient nutrient remobilization helps plants conserve resources and supports the growth of new tissues

Unit 9 – Plant Responses to Abiotic Stress

9.1 Drought and salt stress responses

Plants face tough challenges like drought and salt stress. They've evolved clever ways to cope, from closing tiny pores on leaves to growing deeper roots. Hormones like ABA play a key role, triggering responses that help plants save water and protect themselves.

To deal with water loss, plants accumulate special molecules called osmolytes. These help maintain cell balance and protect important structures. Proteins like dehydrins and LEAs also pitch in, acting as molecular bodyguards to shield cells from stress damage.

Physiological Responses

Osmotic Stress and Plant Adaptations

- Osmotic stress occurs when plants experience reduced water availability in the soil due to drought or high salt concentrations
- Stomatal closure is a rapid response to minimize water loss through transpiration (gas exchange pores on leaf surfaces)
- Leaf rolling reduces the surface area exposed to the sun and air, helping to prevent excessive water loss (maize, sorghum)
- Root growth is often enhanced under drought stress to explore deeper soil layers for water and nutrients (increased root-to-shoot ratio)
- Ion homeostasis involves the regulation of ion uptake, transport, and compartmentalization to maintain optimal cellular functions under salt stress

Hormonal Regulation

- Abscisic acid (ABA) is a key plant hormone that mediates various stress responses, including drought and salt stress
- ABA accumulates in response to water deficit and triggers stomatal closure to reduce transpiration and conserve water
- ABA also induces the expression of stress-responsive genes involved in osmotic adjustment, antioxidant defense, and protective protein synthesis
- ABA signaling involves the binding of ABA to receptors (PYR/PYL/RCAR), which leads to the activation of downstream transcription factors (ABFs) and gene expression changes
- Other hormones, such as ethylene and jasmonic acid, also interact with ABA to fine-tune stress responses

Osmotic Adjustment

Osmolyte Accumulation

- Osmolytes are compatible solutes that accumulate in plant cells to maintain osmotic balance and protect cellular components under stress conditions

- Common osmolytes include sugars (trehalose, raffinose), sugar alcohols (mannitol, sorbitol), amino acids (proline), and quaternary ammonium compounds (glycine betaine)
- Osmolyte accumulation lowers the osmotic potential of cells, allowing them to retain water and maintain turgor pressure under drought or salt stress
- Osmolytes also act as osmoprotectants by stabilizing proteins, membranes, and other cellular structures against denaturation and damage

Proline and Aquaporin Regulation

- Proline is a widely studied osmolyte that accumulates in many plant species under stress conditions
- Proline synthesis is upregulated by ABA and involves the activation of key enzymes, such as pyrroline-5-carboxylate synthetase (P5CS)
- Proline acts as an osmolyte, osmoprotectant, and antioxidant, scavenging reactive oxygen species (ROS) generated during stress
- Aquaporins are water channel proteins that facilitate the transport of water across cell membranes
- Under drought stress, the expression and activity of certain aquaporins (PIPs) are downregulated to minimize water loss and maintain cell turgor
- Salt stress can also affect aquaporin function by altering their subcellular localization and gating properties

Protective Proteins

Dehydrins and LEA Proteins

- Dehydrins are a family of intrinsically disordered proteins that accumulate in response to dehydration, low temperature, and osmotic stress
- Dehydrins act as molecular chaperones, stabilizing proteins and membranes against denaturation and aggregation under stress conditions
- LEA (Late Embryogenesis Abundant) proteins are another group of hydrophilic proteins that accumulate during seed maturation and in vegetative tissues under stress
- LEA proteins are classified into several families (LEA1-LEA5) based on their amino acid sequences and conserved motifs
- Like dehydrins, LEA proteins function as molecular chaperones and osmolytes, protecting cellular components from damage during dehydration and osmotic stress
- Some LEA proteins also exhibit antioxidant properties, scavenging ROS and preventing oxidative damage to proteins and membranes

9.2 Temperature stress: heat and cold

Plants face temperature extremes that can disrupt their normal functions. Heat stress triggers protective mechanisms like heat shock proteins and membrane adaptations. Cold stress prompts acclimation responses, including antifreeze proteins and dehydrins.

Understanding these responses is crucial for plant survival in changing climates. From cellular protection to whole-plant adaptations, temperature stress responses showcase plants' remarkable ability to cope with environmental challenges.

Heat Stress Response

Cellular Protection Mechanisms

- Heat shock proteins (HSPs) are rapidly synthesized in response to heat stress
- Act as molecular chaperones to prevent protein denaturation and aggregation
- Assist in refolding of denatured proteins to maintain cellular function
- Major classes include HSP60, HSP70, HSP90, and small HSPs
- Membrane fluidity increases at high temperatures due to changes in lipid composition
- Leads to increased permeability and potential loss of cellular contents
- Plants adapt by altering fatty acid saturation levels to maintain optimal fluidity
- Involves enzymes such as desaturases and elongases to modify membrane lipids
- Reactive oxygen species (ROS) production is enhanced under heat stress conditions
- Includes superoxide radicals, hydrogen peroxide, and hydroxyl radicals
- Can cause oxidative damage to proteins, lipids, and DNA
- Plants employ antioxidant defense systems to scavenge ROS (superoxide dismutase, catalase, ascorbate peroxidase)
- Compatible solutes (proline, glycine betaine) also contribute to ROS detoxification

Cold Acclimation and Vernalization

Adaptive Responses to Low Temperatures

- Cold acclimation is the gradual acquisition of freezing tolerance upon exposure to low non-freezing temperatures
- Involves changes in gene expression, metabolite accumulation, and membrane composition
- Enhances survival during subsequent freezing events by minimizing cellular damage
- Examples include increased synthesis of cryoprotectants (sugars, proline) and antifreeze proteins
- Vernalization is the promotion of flowering by prolonged exposure to cold temperatures
- Required by many winter annual and biennial plants to transition from vegetative to reproductive growth
- Involves epigenetic silencing of floral repressors (FLC in Arabidopsis) by chromatin modifications
- Ensures flowering occurs under favorable conditions in spring after winter cold exposure
- CBF/DREB transcription factors play a central role in cold acclimation and freezing tolerance
- Bind to C-repeat/Dehydration-Responsive Elements (CRT/DRE) in promoters of cold-responsive genes

- Rapidly induced by low temperatures to activate downstream genes involved in cold protection
- Overexpression of CBF/DREB factors enhances freezing tolerance in various plant species (Arabidopsis, tomato, barley)

Cold Stress Protection

Mechanisms to Mitigate Freezing Damage

- Antifreeze proteins (AFPs) accumulate in cold-acclimated plants to prevent ice crystal growth
- Bind to ice crystal surfaces and inhibit their expansion, reducing cellular damage
- Present in various overwintering plants (winter rye, carrot, bittersweet nightshade)
- Can be induced by both cold acclimation and vernalization treatments
- Dehydrins are a class of late embryogenesis abundant (LEA) proteins that protect cells from dehydration stress
- Accumulate in response to cold, drought, and salinity stress to stabilize membranes and proteins
- Act as molecular chaperones to prevent protein aggregation under dehydration conditions
- Examples include COR15a in Arabidopsis and WCOR410 in wheat, induced by low temperatures
- Chilling injury occurs in sensitive plants exposed to low non-freezing temperatures (0-15°C)
- Leads to membrane dysfunction, electrolyte leakage, and reduced photosynthetic capacity
- Symptoms include wilting, chlorosis, necrosis, and pitting of fruits and vegetables (tomato, cucumber, banana)
- Can be mitigated by pre-conditioning treatments, controlled atmosphere storage, and genetic improvement of chilling tolerance

9.3 Light stress and photoprotection mechanisms

Photoinhibition and Photoprotection

Photoinhibition and its consequences

When a plant absorbs more light energy than it can use for photosynthesis, the excess energy has to go somewhere. That's the core problem behind photoinhibition: the photosynthetic apparatus gets overwhelmed, and photosynthetic efficiency drops.

The most vulnerable target is the D1 protein in the photosystem II (PSII) reaction center. Excess excitation energy damages D1 faster than the cell can replace it, which bottlenecks electron transport through PSII.

The downstream consequences compound quickly:

- Excess energy that isn't quenched generates reactive oxygen species (ROS), especially singlet oxygen ($^1O_2$), right at the PSII reaction center
- Singlet oxygen is highly reactive and damages lipids, proteins, and DNA in the chloroplast
- Prolonged photoinhibition reduces overall carbon fixation, slowing growth and lowering productivity

Photoprotective mechanisms

Plants have several ways to deal with excess light before damage occurs.

Non-photochemical quenching (NPQ) is the primary line of defense. Instead of driving photochemistry, excess absorbed light energy is safely released as heat. The xanthophyll cycle is central to how NPQ works:

1. Under normal light, the carotenoid pigment violaxanthin predominates in the thylakoid membrane.

2. When light becomes excessive, violaxanthin is enzymatically converted to antheraxanthin and then to zeaxanthin.

3. Zeaxanthin accepts excess excitation energy from chlorophyll molecules and dissipates it as heat, preventing that energy from generating ROS.

4. When light intensity drops again, zeaxanthin is converted back to violaxanthin.

This cycle is driven by the pH gradient across the thylakoid membrane: high light increases the ΔpH, which activates the enzyme violaxanthin de-epoxidase.

The PSII repair cycle is a separate but equally important mechanism. Since D1 damage is essentially unavoidable under bright light, the cell continuously degrades damaged D1 proteins and inserts newly synthesized copies into the PSII complex. This turnover keeps PSII functional even during sustained high-light exposure. Photoinhibition becomes a real problem only when the rate of D1 damage outpaces the rate of repair.

Cellular Responses to Light Stress

Chloroplast movement

Chloroplasts aren't fixed in place. They actively reposition themselves within the cell depending on light intensity, a process called chloroplast photorelocation.

- Low light (accumulation response): Chloroplasts spread out along the cell walls perpendicular to the incoming light, maximizing the surface area that intercepts photons.

- High light (avoidance response): Chloroplasts migrate to the cell walls parallel to the incoming light, essentially turning edge-on to the beam. This reduces the cross-section exposed to excess light and lowers the risk of photodamage.

This movement depends on the actin cytoskeleton and is triggered by blue light receptors called phototropins (phot1 and phot2). Phot2 is particularly important for the avoidance response under high light.

Antioxidant systems

Even with NPQ and chloroplast movement, some ROS production is inevitable during light stress. Antioxidant systems serve as the cleanup crew, neutralizing ROS before they cause widespread oxidative damage.

Enzymatic antioxidants directly scavenge specific ROS:

- Superoxide dismutase (SOD) converts superoxide radicals (O_2^-) into hydrogen peroxide (H_2O_2)

- Ascorbate peroxidase (APX) and catalase (CAT) then break down H_2O_2 into water and oxygen

Non-enzymatic antioxidants also contribute:

- Ascorbate (vitamin C) and glutathione are water-soluble antioxidants that donate electrons to neutralize ROS
- Tocopherols (vitamin E) are lipid-soluble and protect membrane lipids from peroxidation by quenching singlet oxygen and lipid radicals

These components are linked through the ascorbate-glutathione cycle (also called the Halliwell-Asada cycle). In this pathway, APX uses ascorbate to reduce H_2O_2, and the oxidized ascorbate is regenerated using glutathione, which is in turn regenerated by glutathione reductase using NADPH. This cycle keeps the antioxidant pool recycled and functional.

State transitions

State transitions address a different problem from NPQ: not too much total light, but an imbalance in how light energy is distributed between the two photosystems.

Because PSI and PSII have slightly different absorption spectra, changing light quality (not just intensity) can over-excite one photosystem relative to the other. State transitions correct this:

- State 2: When PSII is over-excited (the plastoquinone pool becomes over-reduced), the kinase STN7 phosphorylates LHCII (the light-harvesting complex of PSII). Phosphorylated LHCII detaches from PSII and associates with PSI, redirecting energy toward PSI.
- State 1: When PSI is over-excited (the plastoquinone pool becomes more oxidized), a phosphatase dephosphorylates LHCII, which migrates back to PSII.

The redox state of the plastoquinone pool acts as the sensor: a reduced pool signals PSII over-excitation, while an oxidized pool signals the opposite. The cytochrome b_6f complex activates the STN7 kinase in response to plastoquinone reduction.

State transitions are a relatively short-term adjustment. They fine-tune energy distribution under moderate, fluctuating light rather than providing protection against severe excess light.

UV-B Stress

UV-B radiation and its effects on plants

UV-B radiation (wavelengths 280–315 nm) carries enough energy per photon to directly damage biological molecules, making it a distinct stress from visible-light excess.

- UV-B causes direct DNA damage by inducing pyrimidine dimers (covalent bonds between adjacent pyrimidines on the same DNA strand). These distort the double helix and block replication and transcription if not repaired.
- UV-B also generates ROS, adding oxidative stress on top of the direct molecular damage.
- The combined effects reduce photosynthetic efficiency, inhibit growth, and can lower crop yield.

Protective mechanisms against UV-B stress

Plants defend against UV-B primarily by producing UV-screening compounds that absorb UV-B in the epidermis before it reaches the photosynthetic mesophyll cells below.

Flavonoids are the most important class of UV screens:

- These phenolic compounds accumulate in epidermal cells and vacuoles, forming a chemical sunscreen layer

• Key UV-absorbing flavonoids include quercetin, kaempferol, and anthocyanins (which also produce the red, blue, and purple pigments you see in many plants)

Other UV-screening compounds include sinapate esters (such as sinapoyl malate, particularly important in Arabidopsis and other Brassicaceae) and hydroxycinnamic acid derivatives, which absorb strongly in the UV range.

The production of these compounds is regulated by the UV-B photoreceptor UVR8 (UV RESISTANCE LOCUS 8). Here's how the signaling works:

1. UV-B causes the UVR8 homodimer to monomerize.

2. UVR8 monomers interact with the E3 ubiquitin ligase COP1.

3. The UVR8-COP1 complex activates transcription factors (notably HY5) that upregulate genes in the flavonoid biosynthesis pathway.

4. Flavonoids and other UV-screening compounds accumulate in the epidermis.

This means UV-B exposure itself triggers the protective response, allowing plants to acclimate to UV-B levels in their environment.

9.4 Heavy metal toxicity and oxidative stress

Metal-Binding Proteins

Heavy metals like cadmium, lead, and mercury are toxic to plant cells because they displace essential metal cofactors, denature proteins, and trigger oxidative damage. Plants defend themselves by binding these metals to specialized molecules and locking them away where they can't cause harm.

Phytochelatins and Metallothioneins

Phytochelatins are small, cysteine-rich peptides that plants synthesize specifically in response to heavy metal exposure. They're built from glutathione (a tripeptide of glutamate, cysteine, and glycine), and their thiol (-SH) groups on cysteine residues bind tightly to metal ions like cadmium, lead, and mercury. By chelating these metals, phytochelatins reduce the concentration of free toxic ions in the cytoplasm.

Metallothioneins are low molecular weight, cysteine-rich proteins found across plants, animals, and fungi. Unlike phytochelatins, metallothioneins are gene-encoded rather than enzymatically synthesized. In plants, they contribute to homeostasis and detoxification of metals such as copper, zinc, and cadmium. Different metallothionein isoforms show tissue-specific expression patterns, suggesting they serve distinct roles in metal handling throughout the plant.

Metal Chelation and Vacuolar Sequestration

Metal chelation is the binding of metal ions to organic compounds, forming stable complexes that reduce the metal's bioavailability and toxicity. Several organic molecules serve as chelators in plants:

• Organic acids like citrate and malate bind metals in the cytoplasm and xylem sap

• Nicotianamine, a non-proteinogenic amino acid, is particularly important for chelating iron and zinc during long-distance transport

Vacuolar sequestration is the final step in many detoxification pathways. Once metals are chelated (often as metal-phytochelatin complexes), they're transported into the vacuole by ATP-binding cassette (ABC) transporters. The vacuole acts as a safe storage compartment, isolating toxic metals from sensitive organelles like chloroplasts and mitochondria.

Some species are remarkably good at this. Thlaspi caerulescens sequesters cadmium, and Arabidopsis halleri handles zinc, both relying heavily on efficient vacuolar compartmentalization.

Oxidative Stress Response

Reactive Oxygen Species (ROS) and Antioxidant Enzymes

Heavy metals generate reactive oxygen species (ROS) through multiple routes. Redox-active metals like iron and copper catalyze Fenton reactions ($Fe^{2+} + H_2O_2 \rightarrow Fe^{3+} + OH^{\bullet} + OH^{-}$), directly producing hydroxyl radicals. Non-redox-active metals like cadmium and lead cause ROS indirectly by displacing essential metal cofactors from enzymes or by depleting glutathione pools.

The major ROS species you need to know:

- Superoxide ($O_2^{\bullet -}$)
- Hydrogen peroxide (H_2O_2)
- Hydroxyl radical ($OH^{\bullet}$), the most reactive and damaging

These molecules damage proteins, peroxidize membrane lipids, and cause DNA strand breaks. Plants counter them with a layered antioxidant enzyme system:

Superoxide dismutase (SOD) catalyzes the first line of defense, converting superoxide to hydrogen peroxide and oxygen. Three isoforms exist, each with a different metal cofactor: Cu/Zn-SOD (cytoplasm, chloroplasts), Mn-SOD (mitochondria), and Fe-SOD (chloroplasts). Overexpression of SOD in Arabidopsis thaliana and Nicotiana tabacum has been shown to improve heavy metal tolerance.

Catalase decomposes H_2O_2 into water and oxygen. It's located primarily in peroxisomes, where it handles H_2O_2 generated by photorespiration and fatty acid β-oxidation.

Peroxidases reduce H_2O_2 using various electron donors:

- Ascorbate peroxidase (APX) uses ascorbate as its electron donor and is a central enzyme in the ascorbate-glutathione cycle
- Glutathione peroxidase (GPX) uses glutathione and is especially important for detoxifying lipid hydroperoxides in membranes

Antioxidant Molecules

Glutathione and Ascorbate

These two molecules work together in the ascorbate-glutathione cycle (also called the Halliwell-Asada cycle), the primary pathway for H_2O_2 detoxification in chloroplasts and the cytoplasm.

Glutathione (GSH) is the same tripeptide (glutamate-cysteine-glycine) that serves as the precursor for phytochelatin synthesis. It plays a dual role under heavy metal stress: it's both a building block for metal-binding peptides and a direct antioxidant. Here's how the redox cycle works:

1. Reduced glutathione (GSH) donates electrons to GPX or glutathione S-transferase (GST), scavenging ROS or conjugating toxic compounds
2. This produces oxidized glutathione (GSSG)

3. Glutathione reductase (GR) regenerates GSH from GSSG, using NADPH as the electron donor

The GSH:GSSG ratio is a key indicator of cellular redox status. A dropping ratio signals oxidative stress.

Ascorbate (vitamin C) is a water-soluble antioxidant that connects directly to glutathione through the cycle:

1. APX uses ascorbate to reduce H_2O_2 to water, producing monodehydroascorbate (MDHA)

2. MDHA can be reduced back to ascorbate by monodehydroascorbate reductase (MDHAR), or it spontaneously disproportionates to dehydroascorbate (DHA)

3. Dehydroascorbate reductase (DHAR) regenerates ascorbate from DHA, using glutathione as the electron donor

Ascorbate can also directly scavenge superoxide, H_2O_2, and hydroxyl radicals outside the cycle. Plants like spinach and kiwifruit maintain particularly high ascorbate pools.

Phytoremediation

Using Plants to Clean Up Heavy Metal Contamination

Phytoremediation applies everything covered above to an environmental problem: using plants to remove or neutralize heavy metal contaminants from soil and water. There are three main strategies:

- Phytoextraction: Plants absorb metals through their roots and accumulate them in above-ground shoots and leaves. The biomass is then harvested and safely disposed of or processed to recover the metals.

- Phytostabilization: Plants reduce metal mobility in soil through root exudates that change soil pH and chemistry, preventing metals from leaching into groundwater. The metals stay in place but become less bioavailable.

- Phytovolatilization: Plants convert certain metals (notably selenium and mercury) into volatile forms that are released into the atmosphere.

Hyperaccumulator plants are species that tolerate and accumulate metal concentrations 100 to 1,000 times higher than normal plants. Notable examples:

- Noccaea caerulescens (formerly Thlaspi): cadmium and zinc

- Pteris vittata (brake fern): arsenic

- Alyssum murale: nickel

These species achieve this through enhanced root uptake transporters, efficient xylem loading for root-to-shoot translocation, and robust vacuolar sequestration in leaf cells.

Genetic engineering can extend these capabilities to faster-growing, higher-biomass species. Transgenic approaches include:

- Expressing metal-binding proteins (phytochelatins, metallothioneins) or metal transporters in non-accumulator species

- Transgenic Arabidopsis expressing yeast metallothionein genes (CUP1, CRS5) showed improved copper tolerance

- Transgenic tobacco expressing a bacterial mercuric reductase gene (merA) could convert toxic Hg^{2+} to less toxic volatile Hg^0, combining detoxification with phytovolatilization

Unit 10 – Plant Defenses and Biotic Interactions

10.1 Plant immune system and pathogen recognition

Plants have a sophisticated immune system to protect against pathogens. They use pattern recognition receptors to detect conserved pathogen molecules, triggering initial defenses. If pathogens bypass this, plants employ resistance genes to recognize specific pathogen proteins and mount a stronger response.

Plants defend themselves through various mechanisms. These include the hypersensitive response, which involves localized cell death, and cell wall reinforcement to create physical barriers. Plants also produce antimicrobial compounds and phytoalexins to directly combat invading pathogens.

Pathogen Recognition and Immune Responses

Pattern Recognition Receptors and PAMPs

- Plants have evolved pattern recognition receptors (PRRs) to detect conserved pathogen-associated molecular patterns (PAMPs) and trigger immune responses
- PAMPs consist of essential microbial structures such as bacterial flagellin, lipopolysaccharides, and fungal chitin
- PRRs are typically receptor-like kinases or receptor-like proteins located on the plant cell surface
- Examples of well-characterized PRRs include FLS2 (recognizes bacterial flagellin) and CERK1 (recognizes fungal chitin)
- Recognition of PAMPs by PRRs activates PAMP-triggered immunity (PTI), the first layer of plant defense

Effector-Triggered Immunity and R Genes

- Pathogens secrete effector proteins to suppress PTI and promote virulence
- Plants have evolved resistance (R) genes that encode intracellular nucleotide-binding leucine-rich repeat (NB-LRR) proteins to recognize specific pathogen effectors
- Recognition of effectors by R proteins activates effector-triggered immunity (ETI), a more rapid and robust defense response compared to PTI
- ETI often leads to a hypersensitive response, characterized by localized cell death at the infection site to limit pathogen spread
- Examples of R genes include RPM1 (recognizes Pseudomonas syringae effector AvrRpm1) and N (recognizes tobacco mosaic virus replicase)

Defense Mechanisms

Hypersensitive Response and Cell Wall Reinforcement

- The hypersensitive response is a form of programmed cell death that occurs at the site of pathogen infection to limit pathogen spread

- It involves the rapid accumulation of reactive oxygen species, activation of defense genes, and localized cell death
- Plants reinforce their cell walls by depositing callose, lignin, and other structural proteins to create a physical barrier against pathogen invasion
- Callose deposition is triggered by the activation of callose synthase enzymes and can occlude plasmodesmata to restrict pathogen movement between cells

Antimicrobial Compounds and Phytoalexins

- Plants produce a diverse array of antimicrobial compounds to defend against pathogens
- These include pathogenesis-related (PR) proteins such as chitinases and glucanases that degrade fungal cell walls
- Plants also synthesize small molecule antimicrobial compounds called phytoalexins in response to pathogen attack
- Phytoalexins are low molecular weight, lipophilic compounds that accumulate rapidly at the infection site and exhibit broad-spectrum antimicrobial activity
- Examples of phytoalexins include camalexin (Arabidopsis), resveratrol (grapes), and glyceollin (soybeans)

10.2 Induced defenses and systemic acquired resistance

Plants have clever defense strategies against pathogens. Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are two key mechanisms. These responses help plants fight off invaders throughout their entire body, not just at the infection site.

SAR and ISR work differently but both boost plant immunity. SAR uses salicylic acid as a signal, while ISR relies on jasmonic acid and ethylene. Understanding how these pathways interact helps scientists develop tougher crops that can fend off various threats.

Systemic Acquired Resistance (SAR)

SAR Activation and Signaling

- Systemic acquired resistance (SAR) is a broad-spectrum, long-lasting defense response triggered by a localized infection that provides enhanced resistance against subsequent pathogen attacks throughout the plant
- SAR is activated by the accumulation of salicylic acid (SA) at the site of infection which acts as a signaling molecule to induce defense responses in distal tissues
- SA accumulation leads to the activation of nonexpresser of pathogenesis-related genes 1 (NPR1), a key regulator of SAR that acts as a transcriptional coactivator to induce the expression of defense-related genes (PR genes)
- NPR1 exists as an oligomer in the cytosol under normal conditions but upon SA accumulation, NPR1 monomers are released and translocate to the nucleus where they interact with transcription factors to activate PR gene expression

SAR-Induced Defense Responses

- SAR induces the expression of pathogenesis-related (PR) proteins which have antimicrobial properties and help limit pathogen spread
- Examples of PR proteins include chitinases (degrade fungal cell walls), β-1,3-glucanases (degrade fungal cell walls), and thaumatin-like proteins (disrupt fungal membranes)
- SAR also leads to the accumulation of phytoalexins, low molecular weight antimicrobial compounds that inhibit pathogen growth and development
- Examples of phytoalexins include camalexin (Arabidopsis), medicarpin (alfalfa), and glyceollin (soybean)
- SAR can provide long-lasting protection against a broad spectrum of pathogens including fungi, bacteria, and viruses for several weeks to months after the initial infection

Induced Systemic Resistance (ISR)

ISR Activation and Signaling

- Induced systemic resistance (ISR) is a defense response triggered by beneficial microbes such as plant growth-promoting rhizobacteria (PGPR) and fungi that provides enhanced resistance against subsequent pathogen attacks
- ISR is mediated by the plant hormones jasmonic acid (JA) and ethylene (ET) which act as signaling molecules to activate defense responses in distal tissues
- JA and ET accumulate in response to beneficial microbe colonization and activate transcription factors such as ERF1 and MYC2 which regulate the expression of defense-related genes
- ISR does not involve the accumulation of PR proteins or SA, distinguishing it from SAR

ISR-Induced Defense Responses

- ISR induces the expression of defense-related genes such as PDF1.2 (plant defensin), HEL (hevein-like protein), and CHI-B (chitinase B) which have antimicrobial properties
- ISR also leads to the priming of defense responses, allowing plants to respond more quickly and strongly to subsequent pathogen attacks
- Priming involves the accumulation of inactive forms of defense-related proteins and transcripts that can be rapidly activated upon pathogen challenge
- ISR can provide protection against a range of pathogens including fungi, bacteria, and insects
- Examples of ISR-inducing microbes include Pseudomonas fluorescens (bacteria) and Trichoderma harzianum (fungus)

Interactions Between Defense Pathways

Cross-Talk Between SA and JA/ET Signaling

- Cross-talk between the SA and JA/ET signaling pathways allows plants to fine-tune their defense responses based on the type of pathogen encountered

- SA and JA/ET signaling are often antagonistic, with activation of one pathway suppressing the other
- For example, SA accumulation during SAR can suppress JA-mediated defenses against herbivores and necrotrophic pathogens
- However, synergistic interactions between SA and JA/ET signaling have also been observed, particularly during early stages of infection
- For example, both SA and JA accumulate during the hypersensitive response (HR) to biotrophic pathogens
- The timing, magnitude, and spatial distribution of SA and JA/ET accumulation likely determines the outcome of their interactions and the ultimate defense response mounted by the plant

Integration of Defense Responses

- Plants must integrate signals from multiple defense pathways to optimize their response to the current threat environment
- The balance between SA and JA/ET signaling is influenced by factors such as the type of pathogen (biotrophic vs. necrotrophic), the stage of infection (early vs. late), and environmental conditions (light, temperature, humidity)
- Other plant hormones such as abscisic acid (ABA), auxins, cytokinins, and gibberellins can also modulate SA and JA/ET signaling and influence the outcome of plant-pathogen interactions
- Understanding the complex interactions between defense signaling pathways is crucial for developing crops with enhanced resistance to a broad spectrum of pathogens

10.3 Plant-herbivore interactions

Plants have evolved clever ways to defend themselves against hungry herbivores. From physical barriers like thorns to chemical weapons like toxins, they use a variety of strategies to stay alive and thrive.

These defenses can be always-on or activated when needed. Some even call for backup, releasing smells that attract predators to eat the herbivores. It's a complex dance of survival in the plant world.

Plant Defense Strategies

Types of Plant Defenses

- Constitutive defenses are always present in the plant, regardless of whether the plant is under attack by herbivores or pathogens
- These defenses are typically physical barriers or chemical compounds that deter or prevent damage from herbivores (thorns, trichomes, thick cuticles)
- Inducible defenses are activated only in response to damage or stress, such as herbivory or pathogen attack
- These defenses often involve the production of toxic or deterrent compounds, or the release of volatile organic compounds that attract natural enemies of the herbivore (protease inhibitors, polyphenol oxidases, volatile organic compounds)

Modes of Action for Plant Defenses

- Direct defenses directly affect the herbivore by deterring feeding, reducing digestibility, or causing toxicity
- Examples include physical barriers like thorns and trichomes, as well as chemical defenses like alkaloids, terpenes, and phenolics that can be toxic or unpalatable to herbivores
- Indirect defenses promote the effectiveness of the natural enemies of herbivores, such as predators and parasitoids
- Plants emit volatile organic compounds (VOCs) that attract predators and parasitoids of the herbivores, increasing the mortality of the herbivores and reducing plant damage (methyl salicylate, methyl jasmonate, green leaf volatiles)

Physical and Chemical Defenses

Structural Defenses

- Trichomes are hair-like structures on the surface of leaves, stems, and other plant organs that can deter herbivores by physically impeding their movement or by releasing toxic or irritating compounds
- Glandular trichomes contain cells that produce and secrete secondary metabolites, while non-glandular trichomes act as physical barriers (tomato plants, stinging nettles)

Chemical Defenses

- Secondary metabolites are compounds produced by plants that are not essential for primary metabolic processes but play important roles in defense against herbivores and pathogens
- These compounds can be constitutively expressed or induced upon damage and include alkaloids, terpenoids, phenolics, and glucosinolates
- Secondary metabolites can deter feeding, reduce digestibility, or cause toxicity to herbivores (nicotine in tobacco, capsaicin in chili peppers)

Chemical Signaling

Volatile Organic Compounds (VOCs)

- VOCs are small molecular weight compounds that easily evaporate at ambient temperatures and play important roles in plant-plant, plant-herbivore, and plant-predator interactions
- Plants release VOCs in response to herbivore damage, which can induce defense responses in neighboring plants, attract natural enemies of the herbivores, or directly deter herbivore feeding (methyl jasmonate, methyl salicylate, green leaf volatiles)

Herbivore-Induced Plant Volatiles (HIPVs)

- HIPVs are a specific class of VOCs that are emitted by plants in response to herbivore damage and serve to attract predators and parasitoids of the herbivores
- The composition of HIPVs can vary depending on the plant species, the herbivore species, and the type of damage inflicted

• HIPVs can provide important cues for natural enemies to locate their prey or hosts, leading to increased herbivore mortality and reduced plant damage (maize plants emit HIPVs that attract parasitic wasps when attacked by armyworms)

10.4 Beneficial plant-microbe associations

Plants form incredible partnerships with microbes in the soil. These tiny allies help plants access nutrients, fight off diseases, and even convert nitrogen from the air into usable forms. It's like having a secret underground support network!

Mycorrhizal fungi and nitrogen-fixing bacteria are the superstars of these plant-microbe teams. They boost plant growth, improve soil health, and reduce the need for chemical fertilizers. Nature's own sustainable farming system at work!

Mycorrhizal Associations

Symbiotic Relationships Between Plants and Fungi

• Mycorrhizae are symbiotic associations between plant roots and fungi that benefit both partners

• Fungi colonize the plant's roots and extend their hyphae into the surrounding soil, increasing the plant's access to water and nutrients (phosphorus, nitrogen)

• In return, the plant provides the fungus with carbohydrates produced through photosynthesis

• Two main types of mycorrhizae: arbuscular mycorrhizae and ectomycorrhizae

Arbuscular Mycorrhizal Fungi

• Arbuscular mycorrhizal fungi (AMF) are the most common type of mycorrhizae and associate with the majority of land plants

• AMF penetrate the plant's root cells and form highly branched structures called arbuscules within the cells

• Arbuscules are the sites of nutrient exchange between the fungus and the plant

• AMF also produce vesicles, which are storage structures that contain lipids and other nutrients

• Examples of plants that form associations with AMF include legumes (soybeans, alfalfa), grasses (wheat, corn), and many fruit and vegetable crops (tomatoes, potatoes)

Ectomycorrhizae

• Ectomycorrhizae are formed by certain types of fungi, primarily basidiomycetes and ascomycetes, and are associated with woody plants

• Ectomycorrhizal fungi do not penetrate the plant's root cells but instead form a dense network of hyphae around the roots called a mantle

• The fungal hyphae extend into the soil, increasing the plant's access to water and nutrients

• Ectomycorrhizal fungi also form a Hartig net, which is a network of hyphae that grows between the plant's root cells and facilitates nutrient exchange

• Examples of plants that form ectomycorrhizal associations include pine trees, oak trees, and eucalyptus

Nitrogen-Fixing Symbioses

Rhizobia and Legume-Rhizobium Symbiosis

- Rhizobia are soil bacteria that form symbiotic relationships with leguminous plants (beans, peas, alfalfa)
- Rhizobia infect the roots of legumes and stimulate the formation of specialized structures called root nodules
- Within the root nodules, rhizobia convert atmospheric nitrogen (N2) into ammonia (NH3), which the plant can use for growth and development
- In return, the plant provides the rhizobia with carbohydrates and other nutrients

Nodulation Process

- Nodulation is the process by which rhizobia infect the roots of legumes and stimulate the formation of root nodules
- Flavonoids released by the plant roots attract rhizobia and stimulate the expression of nod genes in the bacteria
- Nod factors produced by the rhizobia cause the plant's root hairs to curl and trap the bacteria
- The bacteria enter the root through an infection thread and stimulate the division of root cortical cells, leading to the formation of the nodule
- Inside the nodule, the rhizobia differentiate into bacteroids, which are the nitrogen-fixing form of the bacteria

Nitrogen Fixation

- Nitrogen fixation is the process by which atmospheric nitrogen (N2) is converted into ammonia (NH3), which plants can use for growth and development
- Rhizobia contain the enzyme nitrogenase, which catalyzes the reduction of N2 to NH3
- The plant provides the rhizobia with a low-oxygen environment within the nodule, which is necessary for nitrogenase activity
- The fixed nitrogen is exported from the nodule to the rest of the plant in the form of amino acids and other nitrogen-containing compounds
- Nitrogen fixation by rhizobia is an important source of nitrogen for leguminous crops and reduces the need for synthetic nitrogen fertilizers

Other Beneficial Microbes

Plant Growth-Promoting Rhizobacteria (PGPR)

- PGPR are beneficial bacteria that colonize the rhizosphere (the region of soil surrounding the plant roots) and promote plant growth through various mechanisms
- PGPR can enhance plant growth by producing plant growth regulators such as auxins, cytokinins, and gibberellins

• Some PGPR can solubilize phosphorus and other nutrients, making them more available for plant uptake

• PGPR can also protect plants against pathogens by producing antibiotics, competing for resources, or inducing systemic resistance in the plant

• Examples of PGPR include Pseudomonas, Bacillus, and Azospirillum species

Endophytes

• Endophytes are microorganisms (bacteria or fungi) that live within plant tissues without causing harm to the plant

• Endophytes can colonize various plant parts, including roots, stems, leaves, and seeds

• Some endophytes can promote plant growth by producing plant growth regulators, fixing nitrogen, or solubilizing nutrients

• Endophytes can also protect plants against biotic and abiotic stresses, such as pathogens, insects, drought, and salinity

• Examples of endophytes include Piriformospora indica, a fungus that promotes growth in various crop plants, and Gluconacetobacter diazotrophicus, a nitrogen-fixing bacterium found in sugarcane

Unit 11 – Plant Biotech & Genetic Engineering

11.1 Plant tissue culture and micropropagation

Plant tissue culture harnesses cells' ability to regenerate entire plants. This technique uses small tissue samples (explants) to grow plants in controlled lab conditions, enabling rapid multiplication and genetic manipulation.

Micropropagation, a key application of tissue culture, produces many identical plants quickly. It offers advantages like year-round production and disease-free plants, making it valuable for agriculture and horticulture.

Plant Tissue Culture Basics

Totipotency and Explants

- Totipotency refers to the ability of a single plant cell to regenerate into a whole plant under appropriate conditions
- Nearly all plant cells possess this unique property
- Allows for the regeneration of entire plants from small tissue samples (explants)
- Explants are small pieces of plant tissue used to initiate plant tissue cultures
- Can be obtained from various plant parts (leaves, stems, roots, or meristems)
- Must be carefully selected and excised to ensure successful culture establishment

Callus Formation and Aseptic Technique

- Callus is an unorganized mass of proliferating cells that forms from the explant
- Develops in response to plant growth regulators in the culture medium
- Serves as a source of cells for further differentiation and regeneration
- Aseptic technique is crucial in plant tissue culture to prevent contamination
- Involves sterilizing tools, culture media, and work surfaces
- Explants are surface-sterilized to eliminate microorganisms before culture initiation

Regeneration Pathways

Somatic Embryogenesis

- Somatic embryogenesis is the development of embryos from somatic (non-reproductive) cells
- Mimics the process of zygotic embryogenesis in seeds
- Somatic embryos can develop into complete plants with proper maturation and germination conditions

• Involves inducing embryogenic callus formation and then manipulating culture conditions to promote embryo development

• Plant growth regulators, particularly auxins and cytokinins, play a crucial role in this process

Organogenesis and Meristem Culture

• Organogenesis is the formation of organs (shoots or roots) from callus or directly from explants

• Requires the right balance of plant growth regulators to induce organ formation

• Regenerated shoots can be rooted to produce complete plants

• Meristem culture involves the isolation and culture of apical or axillary meristems

• Meristems are regions of actively dividing cells responsible for plant growth

• Culturing meristems can produce virus-free plants and maintain genetic stability

Micropropagation and Variation

Micropropagation Techniques and Advantages

• Micropropagation is the rapid clonal propagation of plants using tissue culture techniques

• Allows for the production of large numbers of genetically identical plants (clones) from a single parent plant

• Offers several advantages over traditional propagation methods:

• Faster multiplication rates

• Disease-free plant production

• Year-round propagation

• Reduced space requirements

• Micropropagation involves four main stages: 1. Establishment of aseptic cultures 2. Multiplication of shoots 3. Rooting of shoots 4. Acclimatization of plantlets to ex vitro conditions

Plant Growth Regulators and Somaclonal Variation

• Plant growth regulators are essential for controlling growth and development in tissue cultures

• Auxins promote root formation and callus growth

• Cytokinins stimulate shoot formation and cell division

• The right balance of auxins and cytokinins is crucial for successful regeneration

• Somaclonal variation refers to genetic or phenotypic differences among plants derived from tissue culture

• Can arise due to mutations, epigenetic changes, or chromosomal abnormalities during the culture process

• While sometimes undesirable, somaclonal variation can also be a source of novel traits for crop improvement

11.2 Genetic transformation techniques

Genetic transformation techniques are the backbone of plant biotechnology. These methods allow scientists to introduce foreign genes into plants, creating crops with improved traits like disease resistance or enhanced nutrition.

From Agrobacterium-mediated transformation to direct gene transfer methods like biolistics, various approaches enable genetic modification. Understanding the components of transgenes, including promoters and selectable markers, is crucial for successful plant transformation and trait expression.

Agrobacterium-mediated Transformation

Utilizing Agrobacterium's Natural Ability to Transfer DNA

- Agrobacterium-mediated transformation exploits the natural ability of Agrobacterium tumefaciens to transfer DNA into plant cells
- Agrobacterium tumefaciens is a soil bacterium that causes crown gall disease in plants by transferring a portion of its DNA (T-DNA) into the plant genome
- Scientists have modified this natural process to introduce desired genes into plant cells instead of the tumor-inducing genes
- Ti plasmid (tumor-inducing plasmid) is a large plasmid found in Agrobacterium tumefaciens that contains the genes necessary for DNA transfer to plant cells
- The T-DNA region of the Ti plasmid, which is transferred to the plant genome, is modified to carry the desired transgene
- The virulence (vir) genes on the Ti plasmid are responsible for the processing and transfer of the T-DNA into the plant cell

Engineering Agrobacterium for Efficient Gene Transfer

- Binary vector system is a two-plasmid system used to engineer Agrobacterium for gene transfer
- The first plasmid, called the binary vector, contains the T-DNA region with the transgene and selectable markers
- The second plasmid is a disarmed Ti plasmid that contains the vir genes necessary for T-DNA transfer but lacks the tumor-inducing genes
- This separation of the T-DNA and vir genes allows for easier manipulation of the transgene and improved efficiency of gene transfer
- Selectable markers are genes included in the T-DNA that allow for the selection of successfully transformed plant cells
- Common selectable markers include antibiotic resistance genes (kanamycin, hygromycin) and herbicide resistance genes (phosphinothricin)
- Plant cells that have successfully integrated the T-DNA will survive and grow on media containing the corresponding selection agent
- Reporter genes are also included in the T-DNA to visually confirm successful transformation

- Common reporter genes include beta-glucuronidase (GUS) which produces a blue color when stained and green fluorescent protein (GFP) which fluoresces under UV light
- These visual markers allow researchers to quickly identify and isolate transformed plant tissues

Direct Gene Transfer Methods

Biolistics: Bombarding Cells with DNA-Coated Particles

- Biolistics, also known as particle bombardment or gene gun, is a method of directly delivering DNA into plant cells using high-velocity microprojectiles
- DNA is coated onto small metal particles (gold or tungsten) and accelerated towards plant cells using a biolistic device
- The microprojectiles penetrate the cell wall and membrane, carrying the DNA into the cell where it can be integrated into the genome
- Advantages of biolistics include its ability to transform a wide range of plant species and tissues, including those recalcitrant to Agrobacterium-mediated transformation
- Biolistics can be used to transform organelles such as chloroplasts and mitochondria by targeting the DNA to these specific compartments
- This method also allows for the co-transformation of multiple genes simultaneously by coating the particles with different DNA constructs

Electroporation: Using Electrical Pulses to Introduce DNA

- Electroporation is a technique that uses short, high-voltage electrical pulses to create temporary pores in the cell membrane, allowing DNA to enter the cell
- Plant cells are first treated with enzymes to remove the cell wall and create protoplasts (cells without cell walls)
- Protoplasts are then mixed with the DNA and subjected to an electrical pulse, which causes the DNA to enter the cell through the transient pores
- Electroporation is particularly useful for plant species or tissues that are difficult to transform using other methods
- This method can be used to transform a large number of cells simultaneously, increasing the chances of obtaining successful transformants
- However, the regeneration of whole plants from protoplasts can be challenging for some species, limiting the widespread use of electroporation

Transgene Components

Promoters: Controlling Gene Expression

- Promoters are regulatory sequences located upstream of the transgene that control its expression
- Constitutive promoters (CaMV 35S, maize ubiquitin) drive continuous, high-level expression of the transgene in all tissues

- Tissue-specific promoters (seed-specific, root-specific) restrict transgene expression to specific tissues or developmental stages
- Inducible promoters (heat-shock, light-responsive) allow for the controlled expression of the transgene in response to specific environmental or chemical stimuli
- The choice of promoter depends on the desired spatial and temporal expression pattern of the transgene
- For example, using a seed-specific promoter to drive the expression of a nutrient-enhancing gene in the endosperm of cereal grains

Transgene: The Gene of Interest

- The transgene is the gene that is introduced into the plant genome to confer a desired trait or characteristic
- Transgenes can be derived from other plant species, microorganisms, or even animals
- Examples of transgenes include insect resistance genes (Bt toxin), herbicide resistance genes (glyphosate tolerance), and genes for improved nutritional quality (golden rice with increased beta-carotene content)
- The transgene is often codon-optimized to match the preferred codons of the host plant species for improved expression
- Introns may be added to the transgene to enhance its expression by facilitating mRNA processing and export from the nucleus
- Signal peptides can be fused to the transgene to target the protein product to specific cellular compartments (chloroplasts, endoplasmic reticulum) for improved functionality

Selectable Markers: Identifying Transformed Cells

- Selectable markers are genes that are co-introduced with the transgene to allow for the selection of successfully transformed cells
- Antibiotic resistance genes (kanamycin, hygromycin) confer resistance to specific antibiotics, allowing transformed cells to survive and grow on media containing the antibiotic
- Herbicide resistance genes (phosphinothricin, glyphosate) enable transformed cells to tolerate herbicides that would otherwise kill non-transformed cells
- The inclusion of selectable markers is essential for efficiently identifying and isolating transformed cells from a large population of untransformed cells
- Selectable markers are typically driven by constitutive promoters to ensure their expression in all transformed cells
- In some cases, reporter genes (GUS, GFP) are used in conjunction with selectable markers to visually confirm the presence of the transgene in the transformed cells

11.3 Applications of transgenic plants

Transgenic plants revolutionize agriculture by enhancing crop protection, stress tolerance, and nutritional value. These genetically modified organisms offer solutions to challenges like pest resistance, environmental stresses, and nutrient deficiencies, improving food security and sustainability.

From herbicide-resistant crops to biofortified staples like Golden Rice, transgenic plants showcase the potential of genetic engineering in agriculture. They also open new avenues for biopharmaceutical production, demonstrating the diverse applications of plant biotechnology.

Crop Protection

Herbicide Resistance

- Transgenic crops engineered to be resistant to specific herbicides allow for more effective weed control
- Farmers can apply herbicides to fields without damaging the crop, reducing competition from weeds and increasing yield
- Examples of herbicide-resistant crops include Roundup Ready soybeans and corn resistant to glyphosate
- Concerns about the development of herbicide-resistant weeds and the potential environmental impact of increased herbicide use

Insect Resistance

- Crops modified to produce proteins toxic to specific insect pests, reducing the need for insecticide application
- Bt crops, such as Bt cotton and Bt corn, contain genes from the bacterium Bacillus thuringiensis that produce insecticidal proteins
- Bt proteins are toxic to certain insect pests (European corn borer, cotton bollworm) but safe for humans and other animals
- Reduces the use of broad-spectrum insecticides, which can harm beneficial insects and other non-target organisms
- Concerns about the development of insect resistance to Bt proteins and the potential impact on non-target insects

Disease Resistance

- Transgenic plants engineered to resist viral, bacterial, or fungal pathogens, reducing crop losses and the need for pesticide application
- Strategies include introducing genes for antimicrobial proteins, enhancing the plant's immune response, or modifying host-pathogen interactions
- Examples include papaya resistant to papaya ringspot virus and potatoes resistant to late blight (caused by the fungus Phytophthora infestans)
- Potential to reduce the use of fungicides and other pesticides, improving environmental sustainability and food safety

Abiotic Stress Tolerance

Enhancing Resilience to Environmental Stresses

- Transgenic plants designed to withstand abiotic stresses such as drought, salinity, extreme temperatures, and nutrient deficiencies
- Strategies involve introducing genes that confer tolerance to specific stresses or modifying the plant's physiological responses
- Examples include drought-tolerant maize, which expresses genes that help maintain water balance and protect against oxidative stress
- Salt-tolerant rice varieties have been developed by introducing genes that regulate ion transport and osmotic adjustment
- Abiotic stress tolerance can expand the range of environments where crops can be grown and improve yield stability under adverse conditions

Nutritional Improvement

Enhancing Nutritional Content

- Transgenic plants engineered to produce higher levels of essential nutrients, such as vitamins, minerals, and amino acids
- Addresses micronutrient deficiencies in populations that rely on staple crops as their primary food source
- Examples include high-iron rice, high-zinc wheat, and high-provitamin A cassava
- Biofortification through genetic engineering complements conventional breeding efforts and can target specific nutrients

Golden Rice

- Transgenic rice variety engineered to produce beta-carotene, a precursor to vitamin A, in the endosperm
- Addresses vitamin A deficiency, a major public health problem in developing countries that can cause blindness and immune system impairment
- Golden Rice contains genes from daffodil and bacteria that complete the beta-carotene biosynthetic pathway in the rice endosperm
- Potential to improve the health of millions of people who depend on rice as a staple food

Biopharmaceutical Production

Plant-Based Pharmaceuticals

- Transgenic plants used as bioreactors to produce pharmaceutical proteins, such as vaccines, antibodies, and enzymes
- Advantages include lower production costs, scalability, and reduced risk of contamination compared to animal or microbial systems

• Examples include plant-based vaccines for influenza, Ebola, and COVID-19

• Challenges include ensuring consistent product quality, preventing contamination of food crops, and addressing regulatory and public acceptance issues

• Offers a promising platform for the production of affordable and accessible biopharmaceuticals, particularly for developing countries

11.4 Gene editing and CRISPR technology in plants

Gene editing in plants has revolutionized crop improvement. CRISPR-Cas9, a powerful tool, allows precise DNA modifications. This technology enables scientists to enhance plant traits, create disease-resistant varieties, and boost yields, addressing global food security challenges.

CRISPR works by guiding Cas9 enzyme to specific DNA sequences, creating targeted breaks. These breaks are then repaired, introducing desired changes. This process opens up exciting possibilities for developing crops with improved nutritional value and stress tolerance.

CRISPR-Cas9 System Components

CRISPR-Cas9 Mechanism

• Consists of Cas9 endonuclease and a guide RNA (gRNA) that directs Cas9 to a specific DNA sequence

• Cas9 creates a double-strand break (DSB) at the target site, allowing for precise genome editing

• Derived from the adaptive immune system of bacteria and archaea for defense against invading viruses

• Requires a protospacer adjacent motif (PAM) sequence (typically NGG) near the target site for Cas9 recognition and binding

Guide RNA Design

• Guide RNA is a short synthetic RNA that guides Cas9 to the target DNA sequence

• Consists of a scaffold sequence that binds to Cas9 and a 20-nucleotide spacer sequence complementary to the target DNA

• Spacer sequence determines the specificity of the CRISPR-Cas9 system and can be easily designed and synthesized

• Multiple gRNAs can be used simultaneously to target different genomic locations or to increase editing efficiency

Protospacer Adjacent Motif (PAM)

• PAM is a short DNA sequence (typically NGG for Streptococcus pyogenes Cas9) located downstream of the target site

• Essential for Cas9 recognition and binding to the target DNA

• Limits the targetable sites in the genome, as the PAM sequence must be present near the desired editing site

- Alternative Cas9 variants and other CRISPR systems (Cpf1) with different PAM requirements have been developed to expand the range of targetable sequences

DNA Repair Mechanisms

Homology-Directed Repair (HDR)

- HDR is a precise DNA repair pathway that uses a homologous DNA template to repair the double-strand break
- Allows for the introduction of specific mutations, insertions, or deletions at the target site
- Requires the presence of a donor DNA template with homology arms flanking the desired modification
- HDR is less efficient than NHEJ and is primarily active in dividing cells during the S and G2 phases of the cell cycle

Non-Homologous End Joining (NHEJ)

- NHEJ is an error-prone DNA repair pathway that directly ligates the broken DNA ends without using a homologous template
- Often results in small insertions or deletions (indels) at the target site, leading to frameshift mutations and gene knockouts
- NHEJ is the dominant repair pathway in most cell types and is active throughout the cell cycle
- Can be exploited for efficient gene disruption and targeted mutagenesis in plants

Applications and Challenges

Genome Editing Applications

- Targeted gene knockouts and knockins for functional genomics studies in plants
- Introduction of specific mutations to improve crop traits (disease resistance, abiotic stress tolerance, yield)
- Creation of novel alleles and variants for plant breeding and crop improvement
- Development of plant-based bioreactors for producing valuable compounds (biopharmaceuticals, industrial enzymes)

Targeted Mutagenesis Strategies

- CRISPR-Cas9-mediated targeted mutagenesis can be achieved through NHEJ-induced indels or HDR-mediated precise editing
- Multiplexing (targeting multiple genes simultaneously) is possible by using multiple gRNAs
- Base editing (precise single-nucleotide changes) can be achieved using Cas9 nickase fused to a DNA-modifying enzyme (cytidine or adenine deaminase)
- Prime editing (precise insertions, deletions, and substitutions) utilizes a reverse transcriptase-Cas9 fusion and a prime editing guide RNA (pegRNA)

Off-Target Effects and Challenges

- Off-target effects occur when CRISPR-Cas9 induces unintended mutations at sites with sequence similarity to the target site
- Can be minimized by careful gRNA design, using truncated gRNAs, or employing high-fidelity Cas9 variants
- Potential regulatory and public acceptance issues surrounding genetically modified crops and the use of gene editing technologies
- Technical challenges include delivery of CRISPR components to plant cells (Agrobacterium, biolistics, protoplast transfection) and achieving high editing efficiencies in various plant species and genotypes

Unit 12 – Plant Physiology in Agriculture & Ecology

12.1 Crop yield improvement and stress tolerance

Crop yield improvement and stress tolerance are crucial for feeding a growing global population. Scientists use traditional breeding and genetic engineering to enhance harvests, develop resilient plants, and boost nutritional content. These methods aim to create crops that thrive in challenging environments.

Improving abiotic stress tolerance helps plants withstand drought, salt, and heat. Enhancing pest and disease resistance protects crops from harmful organisms. Increasing photosynthetic efficiency and optimizing harvest index can significantly boost yields. These advancements are vital for sustainable agriculture and food security.

Traditional Crop Improvement Methods

Selective Breeding Techniques

- Selective breeding involves choosing the best plants with desired traits to breed and produce offspring with those desired characteristics
- Has been used for thousands of years to improve crop yields, quality, and resistance to pests and diseases
- Includes techniques like mass selection (selecting the best plants from a population), pure-line selection (selecting the best plants from a self-pollinated population), and hybridization (crossing two different varieties to produce offspring with desired traits)
- Examples of crops improved through selective breeding include high-yielding wheat varieties (Norman Borlaug's work) and disease-resistant rice varieties

Optimizing Harvest Index

- Harvest index is the ratio of the yield of a crop to the total plant biomass
- Improving harvest index means increasing the proportion of the plant that is the harvested product (grain, fruit, etc.) compared to the non-harvested parts (stems, leaves, roots)
- Can be improved through breeding and selection for plants with more efficient partitioning of resources to the harvested parts
- Examples include the development of dwarf wheat varieties with a higher harvest index in the Green Revolution and the breeding of rice varieties with more tillers and grains per panicle

Genetic Engineering Techniques

Transgenic Approaches

- Genetic engineering involves the direct manipulation of an organism's DNA to introduce new traits or modify existing ones
- Transgenic approaches involve inserting genes from one species into another to confer desired traits

• Examples include Bt crops (engineered to produce insecticidal proteins from Bacillus thuringiensis) and Golden Rice (engineered to produce beta-carotene to address Vitamin A deficiency)

• Allows for the introduction of traits not possible through traditional breeding, but also raises concerns about ecological impacts and food safety

Other Biotechnology Tools

• Biotechnology encompasses a range of tools and techniques for modifying living organisms for specific purposes

• Includes techniques like marker-assisted selection (using DNA markers to select for desired traits), tissue culture (growing plant cells or tissues in vitro), and genome editing (making precise changes to an organism's DNA)

• Examples include using marker-assisted selection to breed disease-resistant crops and using CRISPR-Cas9 to create non-browning mushrooms and low-gluten wheat

• Offers new opportunities for crop improvement but also requires careful regulation and assessment of potential risks

Abiotic Stress Tolerance

Drought and Salt Tolerance

• Drought tolerance refers to a plant's ability to maintain growth and yield under water-limited conditions

• Salt tolerance refers to a plant's ability to grow and produce in soils with high salt concentrations

• Can be improved through breeding and selection for traits like deep root systems, efficient water use, and accumulation of osmolytes (compounds that help maintain cell turgor under stress)

• Examples include the development of drought-tolerant maize varieties in Africa and the use of wild relatives to breed salt-tolerant wheat and barley

Heat Stress Resistance and Nutrient Use Efficiency

• Heat stress resistance refers to a plant's ability to maintain growth and reproduction at high temperatures

• Nutrient use efficiency refers to a plant's ability to acquire and utilize nutrients (especially nitrogen and phosphorus) for growth and yield

• Can be improved through breeding and selection for traits like heat shock proteins, efficient photosynthesis at high temperatures, and root architecture for nutrient acquisition

• Examples include the development of heat-tolerant cowpea varieties in Africa and the use of mycorrhizal fungi to improve phosphorus uptake in crops

Yield Enhancement Traits

Pest and Disease Resistance

• Pest resistance refers to a plant's ability to withstand or repel insect pests and other herbivores

- Disease resistance refers to a plant's ability to prevent or limit infection by pathogens like fungi, bacteria, and viruses
- Can be improved through breeding and selection for traits like production of defensive compounds, physical barriers to infection, and hypersensitive response to pathogen attack
- Examples include the development of insect-resistant cotton varieties and the use of wild relatives to breed disease-resistant tomatoes and potatoes

Improving Photosynthetic Efficiency

- Photosynthetic efficiency refers to the amount of light energy a plant can convert into biomass through photosynthesis
- Can be improved through breeding and selection for traits like more efficient light capture, faster carbon fixation, and reduced photorespiration
- Examples include the development of C4 rice (engineering rice to use the more efficient C4 photosynthetic pathway) and the use of algal genes to improve photosynthesis in crops
- Improving photosynthetic efficiency has the potential to dramatically increase crop yields, but also requires a deep understanding of the complex processes involved in photosynthesis

12.2 Sustainable agriculture and plant-based solutions

Sustainable agriculture aims to produce food while preserving the environment. It uses methods like organic farming, integrated pest management, and crop rotation to reduce chemical use and maintain soil health. These practices help farmers grow crops sustainably.

Innovative technologies are also transforming farming. Precision agriculture uses data to optimize crop management, while vertical farming allows year-round production in urban areas. Plant-based biofuels offer renewable energy solutions, though challenges remain in balancing food and fuel production.

Sustainable Farming Practices

Organic Farming and Integrated Pest Management

- Organic farming avoids the use of synthetic pesticides, herbicides, and fertilizers
- Relies on natural methods to control pests and maintain soil health (crop rotation, cover crops, and biological pest control)
- Integrated pest management (IPM) combines various pest control strategies to minimize pesticide use
- Includes monitoring pest populations, using resistant crop varieties, and employing targeted pesticide applications only when necessary
- Both organic farming and IPM aim to reduce the environmental impact of agriculture while maintaining crop yields and quality

Crop Rotation and Cover Crops

- Crop rotation involves planting different crops in a specific sequence on the same field over multiple growing seasons
- Helps prevent soil nutrient depletion, reduces pest and disease pressure, and improves soil structure

• Common crop rotation examples include alternating legumes (soybeans, alfalfa) with grains (corn, wheat)

• Cover crops are planted between main crop seasons to protect and improve soil health

• Prevent soil erosion, suppress weeds, and add organic matter to the soil when incorporated

• Examples of cover crops include clover, rye, and radishes

Agroforestry

• Agroforestry integrates trees and shrubs into agricultural systems

• Provides multiple benefits such as soil conservation, carbon sequestration, and enhanced biodiversity

• Examples of agroforestry practices include:

• Alley cropping: growing crops between rows of trees

• Silvopasture: combining trees with livestock grazing

• Windbreaks: planting trees or shrubs to reduce wind erosion and protect crops

Innovative Agricultural Technologies

Precision Agriculture and Sustainable Intensification

• Precision agriculture uses technology to optimize crop management practices

• Involves collecting and analyzing data on soil properties, weather patterns, and crop growth to inform decision-making

• Technologies used include GPS, remote sensing, and variable rate application of inputs (fertilizers, pesticides)

• Sustainable intensification aims to increase agricultural productivity while minimizing environmental impacts

• Focuses on improving resource use efficiency and adopting sustainable farming practices

• Examples include using improved crop varieties, optimizing irrigation, and implementing conservation agriculture techniques (no-till, mulching)

Biofertilizers and Vertical Farming

• Biofertilizers are substances containing living microorganisms that promote plant growth and soil health

• Can reduce the need for synthetic fertilizers and improve nutrient uptake by crops

• Examples of biofertilizers include rhizobia (nitrogen-fixing bacteria) and mycorrhizal fungi

• Vertical farming involves growing crops in vertically stacked layers within controlled environments (indoor farms, greenhouses)

• Allows for year-round crop production, efficient use of space and resources, and reduced transportation costs

• Examples of crops grown in vertical farms include leafy greens, herbs, and strawberries

Renewable Energy Solutions

Plant-based Biofuels

- Plant-based biofuels are renewable energy sources derived from biomass
- Can reduce greenhouse gas emissions and dependence on fossil fuels
- Examples of plant-based biofuels include:
- Ethanol: produced from crops such as corn, sugarcane, and switchgrass
- Biodiesel: made from vegetable oils (soybean, canola) and animal fats
- Biogas: generated through the anaerobic digestion of organic materials (crop residues, manure)
- Challenges associated with plant-based biofuels include competition with food production and potential land-use changes

12.3 Phytoremediation and environmental applications

Plants are nature's cleanup crew. They can absorb, stabilize, and transform harmful contaminants in soil and water. This process, called phytoremediation, uses different plant techniques to tackle various pollutants.

Phytoremediation has real-world applications in cleaning up polluted sites and purifying water. It's a green solution for environmental issues, offering a sustainable alternative to traditional cleanup methods. Plus, it can beautify urban areas while doing the dirty work.

Phytoremediation Techniques

Methods for Removing Contaminants

- Phytoextraction involves plants absorbing contaminants through their roots and translocating them to the shoots and leaves, which can then be harvested and disposed of safely
- Phytostabilization uses plants to immobilize contaminants in the soil, reducing their bioavailability and preventing further spread through erosion or leaching (lead, arsenic)
- Rhizofiltration employs plant roots to absorb and concentrate contaminants from polluted water or wastewater streams, effectively filtering the water (radionuclides, heavy metals)
- Phytovolatilization occurs when plants take up contaminants and release them into the atmosphere through transpiration, converting them into less toxic or harmless forms (mercury, selenium)

Hyperaccumulators and Their Role

- Hyperaccumulators are plants that can tolerate and accumulate exceptionally high levels of contaminants, such as heavy metals, in their tissues without suffering adverse effects
- Examples include Thlaspi caerulescens for cadmium and zinc, and Pteris vittata for arsenic
- These plants have evolved specialized mechanisms for enhanced uptake, translocation, and sequestration of contaminants in their above-ground biomass
- Hyperaccumulators are valuable tools in phytoremediation as they can efficiently remove contaminants from soil and water, making the process more effective and economical compared to

traditional remediation methods (excavation, chemical treatment)

Environmental Applications

Bioremediation and Pollution Control

- Bioremediation utilizes living organisms, such as plants and microbes, to degrade, transform, or detoxify contaminants in soil, water, and air
- Phytoremediation is a type of bioremediation that specifically employs plants to clean up contaminated sites
- Heavy metal contamination, resulting from industrial activities, mining, and improper waste disposal, poses significant environmental and health risks
- Plants can accumulate and sequester heavy metals (cadmium, lead, mercury) in their tissues, reducing their concentration in the environment
- Soil pollution, caused by organic pollutants (pesticides, hydrocarbons) and inorganic contaminants (heavy metals, salts), can be mitigated through phytoremediation techniques
- Plants can degrade organic pollutants through their metabolic processes and immobilize inorganic contaminants in the root zone

Water Purification and Green Infrastructure

- Phytoremediation can be applied to water purification, using aquatic plants (water hyacinth, cattails) to absorb and accumulate contaminants from polluted water bodies (rivers, lakes, wetlands)
- Constructed wetlands and floating plant systems can effectively treat wastewater, removing nutrients, pathogens, and other pollutants
- Green infrastructure incorporates phytoremediation principles to create sustainable and eco-friendly solutions for urban environments
- Examples include green roofs, which use plants to absorb pollutants and reduce stormwater runoff, and bioswales, which are vegetated channels designed to filter and treat polluted runoff from roads and parking lots
- Integrating phytoremediation into urban landscapes not only helps mitigate pollution but also provides additional benefits such as improving air quality, reducing urban heat island effect, and enhancing biodiversity

12.4 Climate change impacts on plant physiology and adaptation

Climate change is messing with plants big time. Rising CO_2, warmer temps, and crazy weather are changing how plants grow, reproduce, and survive. It's a whole new ballgame for our green friends.

Plants are trying to adapt, but it's not easy. Some are blooming earlier, moving to new areas, or evolving new traits. These changes ripple through ecosystems, affecting everything from pollinators to carbon storage.

Climate Change Factors

Atmospheric CO_2 Concentration

• Atmospheric CO_2 levels have risen from pre-industrial levels of 280 ppm to over 400 ppm today due to anthropogenic activities (fossil fuel combustion, deforestation)

• Elevated CO_2 directly affects plant physiology by increasing photosynthetic rates and water use efficiency

• Higher CO_2 concentrations can lead to enhanced plant growth and biomass accumulation, particularly in C3 plants (wheat, rice, soybeans)

• Elevated CO_2 may also alter plant nutrient content and secondary metabolite production, affecting herbivory and plant-insect interactions

Global Temperature Rise

• Average global temperatures have increased by approximately 1°C since pre-industrial times, with projections of further warming by 1.5-4°C by 2100

• Warmer temperatures can extend growing seasons, accelerate plant development, and shift geographical ranges of plant species

• Heat stress can impair photosynthesis, cause oxidative damage, and disrupt reproductive processes in plants, particularly during sensitive stages (flowering, fruit set)

• Rising temperatures may also increase evapotranspiration rates, exacerbating drought stress in water-limited environments

Intensification of Extreme Weather Events

• Climate change is expected to increase the frequency and severity of extreme weather events such as droughts, floods, and heatwaves

• Prolonged droughts can lead to plant water stress, reduced growth, and increased mortality, particularly in non-irrigated systems

• Flooding can cause soil waterlogging, oxygen deprivation, and nutrient leaching, negatively impacting plant growth and survival

• Heatwaves can cause heat stress, leaf scorching, and accelerated senescence, reducing crop yields and plant fitness

• Extreme weather events can also disrupt plant phenology, pollination, and seed dispersal, affecting plant reproductive success

Plant Responses and Adaptations

Phenological Shifts and Range Expansion

• Plants may respond to changing climatic conditions by adjusting their timing of growth and development (phenology)

• Warmer temperatures can advance spring leaf-out and flowering times, while delayed autumn senescence can extend growing seasons

- Species may also shift their geographical ranges to track suitable climatic conditions, with poleward and upward elevational shifts observed in many plant communities
- Range shifts can lead to the formation of novel plant assemblages and alter biotic interactions (competition, herbivory, pollination)

Enhanced Carbon Sequestration and Adaptive Evolution

- Elevated CO_2 can stimulate plant photosynthesis and carbon uptake, potentially increasing terrestrial carbon sequestration
- However, the long-term capacity of plants to act as carbon sinks may be limited by nutrient availability, soil properties, and climate feedbacks
- Plants may also undergo adaptive evolution in response to changing environmental conditions, leading to the emergence of new ecotypes or subspecies
- Rapid evolutionary responses have been observed in traits such as flowering time, drought tolerance, and herbivore resistance in some plant populations

Physiological Plasticity and Acclimation

- Many plant species exhibit physiological plasticity, allowing them to adjust their metabolism and resource allocation in response to environmental cues
- Acclimation to elevated CO_2 can involve changes in photosynthetic capacity, stomatal conductance, and nitrogen use efficiency
- Plants may also acclimate to temperature stress by modifying membrane lipid composition, producing heat shock proteins, and adjusting antioxidant defenses
- Plasticity in root growth and architecture can help plants cope with drought stress by enhancing water and nutrient uptake

Ecological Consequences

Altered Plant-Pollinator Interactions

- Climate change can disrupt the synchrony between plant flowering and pollinator emergence, leading to phenological mismatches
- Earlier flowering in some plant species may cause temporal gaps in floral resource availability for pollinators, affecting their populations and pollination services
- Changes in floral traits (nectar production, scent) under elevated CO_2 or temperature stress may alter pollinator attractiveness and foraging behavior
- Shifts in pollinator ranges or abundances due to climate change can also affect plant reproductive success and gene flow

Changes in Plant Community Composition and Ecosystem Functioning

- Climate change can lead to shifts in plant community composition, with some species becoming more dominant while others decline or go locally extinct
- Differential responses of plant species to elevated CO_2, warming, and drought can alter competitive interactions and successional trajectories

- Changes in plant community composition can have cascading effects on ecosystem processes such as nutrient cycling, water balance, and carbon storage
- Invasive species may benefit from climate change, exploiting disturbed habitats and outcompeting native species, leading to biotic homogenization
- Climate-induced changes in plant communities can affect the structure and functioning of associated animal communities (herbivores, predators) and ecosystem services (pollination, pest control)