I. **PLANT NUTRIENTS**
   
   A. nutrition overview
      1. there are nutrients that plants must obtain from their environment
      2. most nutrients are obtained from the soil
      3. cultivation and fertilization practices affect soil quality
      4. some plants have adaptations to aid survival in areas with nutrient limitations
   
   B. two classes: macronutrients (lots needed) and micronutrients
   
   C. listed as elements, but some elements must be in certain forms to be used
      (example: N works as NO$_3^-$ or NH$_4^+$, not as N$_2$)
   
   D. **macronutrients**
      1. 9 of them: C, O, H, N, K, Ca, Mg, P, S
      2. each usually about 1% or more of dry weight
      3. most abundant C, O (each 44% dry weight), H (6% dry weight)
      4. nitrogen (N) is usually the most limiting factor (plants need lots of it, and in particular forms)
   
   E. **micronutrients**
      1. 7 of them: Cl, Fe, Mn, Zn, B, Cu, Mo
      2. needs range from one to several hundred parts per million
      3. micronutrient needs so small they can be hard to study
   
   F. studies of nutrient deficiencies have revealed diagnostic symptoms (can be used to recommend treatments)

II. **SOIL**
   
   A. natural soil is formed by the breakdown of rocks (weathering of Earth’s outer crust)
   
   B. rocks consist of many different minerals (inorganic compounds of elements)
   
   C. weathering includes physical and biological processes
   
   D. mineral particles
      1. variety of sizes
      2. in most soils, the most abundant particles range from coarse sand with visible particles (up to 2 mm diameter) to clay with very small particles (2 µm or less)
   
   E. soil may also have **humus** – decaying organic material
   
   F. **topsoil** – a mixture of mineral particles, living organisms, and humus
1. where most roots are (some go deeper)
2. **erosion** = loss of topsoil
   - may deprive plants of proper nutrients
   - may deprive plants of consistent water supply
   - may alter downstream environments

G. about half of soil volume spaces or pores, which may have water

H. water in soil
   1. clay holds water very well (electrostatic attraction), often too well
   2. sand allows rapid drainage
   3. best soils typically a mix (called **loams**)

### III. CULTIVATION AND FERTILIZATION

A. natural processes to replace nutrients include decomposition, nitrogen fixation, fire
B. sometimes, plants deplete the nutrients much faster than they can be replaced
C. loss of fertility is a common problem with farms (nutrients leave when plants harvested)
D. farming practices to keep or replenish soil fertility
   1. **crop rotation** – alternating two or more crops that complement each other in nutrient usage and replenishment (example: alternate soybeans, which harbor nitrogen-fixing bacteria, with other crops)
   2. plow under plant material – only remove what you need at harvest
   3. leave fields “fallow” and plow under what grows
   4. **fertilizing** – directly adding nutrients to soil
      - natural/organic (manure, dead animals, plowed under plants)
      - commercial fertilizers
         - usually add N, P, K (numbers indicate percentage)
         - can be expensive; can pollute water supplies and damage ecosystems
      - other nutrients added on case-by-case basis
      - organic fertilizer makes humus, which helps hold water and is usually less polluting of surface waters

### IV. NUTRITIONAL ADAPTATIONS

A. “carnivorous” plants
   1. sandy, acidic soils (like bogs) often have too little nitrogen (and perhaps phosphorus)
2. some plants are adapted to get nutrient supplements from trapped, killed animals
3. Southeastern U.S. is a “hot spot” for such “carnivorous” plants
4. fertilizing these areas can allow other plants to out-compete the carnivorous plants
5. some examples (that you need to be familiar with) follow
6. **Venus flytrap** (*Dionaea muscipula*) – native to coastal Carolinas
   - specialized leaves form trap
   - three sensory hairs each lobe used as triggers
   - brushed hair initiates electrical impulse, leading to a very rapid water accumulation in the outer regions of lobes; trap snaps shut
   - secrete digestive enzymes
   - catch more ants and grasshoppers than flies
7. **sundews** (*Drosera*)
   - trichomes acts as glands, secrete sticky substances
   - leaves often curl around trapped insects, increasing number of insect/trichome contacts
   - digestive enzymes part of trichome secretions
8. **butterworts** (*Penguicula*)
   - glands on leaves secrete sticky substances and digestive enzymes
   - leaves may curl some around captured insects
   - capture mostly gnats
9. **pitcher plants** (*Sarracenia* and others)
   - pitcher-shaped leaves hold water
   - insects (mainly) attracted by colors and “light windows”
   - once inside, hairs pointing down make climbing back up nearly impossible
   - some may secrete digestive enzymes, but other organisms in the pitcher do much of the digestion (mutualisms with bacteria, protists)
10. **bladderworts** (*Utricularia*)
    - traps in aqueous environment (including wet soils)
    - traps are bladder-like leaves that have a spring-like trapdoor
    - secrete digestive enzymes

B. mutualisms
1. **nitrogen-fixing bacteria** – able to convert N\(_2\) to NH\(_3\); often live in specialized root **nodules** in plants types that have this mutualism, especially legumes

2. mycorrhizae – about 90% of vascular plants have these relationships between their roots and certain fungi; important mostly for phosphorous and micronutrient uptake

V. **WATER (and mineral) TRANSPORT**

A. overview – How does water climb a 10-story tree?

1. **capillary action** pulls water partway up tubes
   - thinner tube = greater height
   - but only about 1 meter for xylem width

2. **transpiration** (evaporation of water, mainly from leaves)
   - continuous water column
   - remove water at leaf: negative pressure potential (vacuum)
   - tensile strength of water column = pull water up to replace
   - **water potential** concept
     - higher water potential at roots
     - movement is from high potential to low potential

3. **root pressure** – active transport of ions into roots, leads to water coming in by osmosis

4. net result
   - energy enters system by evaporation (ultimately from sun)
   - energy used to do work of pulling water up against gravity
   - analogous to sucking water up a straw; the stem is the straw
   - energy also provided by plant to push water in (root pressure)

B. absorption by roots

1. most water enters through root hairs (large collective surface area)

2. ions are actively pumped into root hairs
   - proton pumps in root hair plasma membrane
     - work against concentration gradient
     - use ATP for energy to do work
   - concentration higher than in surrounding soil
   - keeps root hairs turgid
   - supplies ions for transport in xylem (more on this later)
3. **osmosis** – water moves into root to alleviate osmotic imbalance
   - enters through cells and intercellular spaces
   - provides positive root pressure that moves water through plant
     - works even without transpiration (even at 100% humidity)
     - can cause **guttation** through special cells in leaves
     - never enough to push water great distances

4. **endodermal barrier**
   - Casparian strips (suberized) block flow to inside, where xylem is
   - water and ions must enter cells of endodermis to get to xylem
   - endodermal cells are selective, controlling what reaches xylem

C. transpiration from leaves
   1. over 90% of water taken up through roots lost to evaporation (most of the rest used in photosynthesis)
   2. mostly, loss is as water vapor through stomata
   3. control of stomata can be critical
      - need water for metabolism and photosynthesis
      - need CO₂ for photosynthesis
      - conflict: open stomata allow CO₂ in, but water vapor out
   4. stomata are controlled by **guard cells**
      - shape changes used for control
      - thicker wall on inside than outside causes “bowing” when turgid
      - turgid when water accumulates, opening stoma
      - **turgor** maintained as follows:
        - active potassium ion uptake by ATP-powered ion channels
        - water enters due to osmotic imbalance
        - required energy typically provided by chloroplasts
      - no energy or wilted plant = loss of turgor = closed stomata
      - generally, stomata open in morning but not evening or night
        (certainly not true for all plants; for example, desert plants)
   5. other factors can regulate transpiration
      - in some species, CO₂ is used
        - high CO₂ → loss of turgor → closed stomata (no need to open)
low CO$_2$ → turgid → open stomata (used by plants like cacti)

- high temperatures (30°C to 34°C) cause stomata to close
- stomata closed during dormancy during dry times
- thick, hard leaves with few stomata = less transpiration
- trichomes – cooler and more humid surface = slower water loss
- pits or crypts – water vapor content in them is higher, slows water loss

D. mineral movement
1. ionic minerals transported with water in xylem
2. entry into xylem controlled through endodermal cells
3. ionic minerals enter roots by an active process
   - roots need oxygen to be able to absorb ions
   - specific ion concentrations in plants higher than in surrounding soil

E. flooding
1. moving water generally not bad, constantly supplies oxygen
2. still water presents problem: depletes oxygen in roots
   - loss of active pumping at root hairs
   - loss of ion entry
   - may dry out leaves (root pressure needed; endoderm greater barrier)
3. adaptations
   - aerenchyma – loose parenchyma with air spaces
     - allow oxygen transport to below-water parts
     - found in water lilies and others
     - may always be present, or formed when needed
   - larger lenticels
   - adventitious roots
   - pneumatophores
     - spongy, air-filled “knees” from roots, emerging from water
     - large lenticels above water allow oxygen to enter
     - cypress knees may be these
     - many mangrove trees have these
     - also help with salt balance
VI. **FOOD (carbohydrate) TRANSPORT**

A. translocation: movement of carbohydrates from where made or stored to where needed

B. storage usually as starch, which must be converted to soluble molecules

C. movement in phloem: how is it studied?
   1. radioactive tracers
   2. aphid stylets
      - aphids pierce into phloem to feed
      - cut off aphid, leaving stylet, and sample phloem

D. movement in phloem: the facts
   1. contents: 10-25% dry matter, almost all sucrose (“syrup”)
   2. moves reasonably fast (up to 1 meter per hour)

E. movement in phloem: how is it done?
   1. **pressure flow hypothesis** (AKA mass-flow or bulk flow)
   2. dissolved carbohydrate flow from **source** to **sink**
   3. **source** – place of dissolved carbohydrate production (leaves, storage organs)
   4. **sink** – place of usage (primarily growing areas – root and stem tips, fruits)
   5. **phloem loading**
      - carbohydrates enter sieve tubes at source by active transport
      - energy for transport comes from companion cells
      - sieve tube water potential lowered
      - creates water potential difference relative to nearby xylem
      - water enters sieve tubes by osmosis
      - increased turgor pressure in sieve tube pushes solution through them
   6. “unloading” at sink
      - removal of carbohydrates leads to drop in turgor pressure
      - drives flow from high water pressure at source to low pressure at sink
      - most of water at sink diffuses back into xylem

VII. **DEVELOPMENTAL STRATEGIES VARY AMONG FUNGI, ANIMALS, AND PLANTS**

A. fungi grow with little specialization, except for reproduction

B. animal development is usually complex but relatively inflexible (also well-studied)

C. plant development
1. cells within plant do not shift positions during development (unlike animals)
2. plants keep growing tips and zones (meristems) – fantastic regeneration capacity
3. plant bodies and structures do not have a fixed size
4. hallmark is flexibility and adaptability outside of basic structural control
5. adaptive development is strongly influenced by the environment

D. overview of plant development
1. embryonic development: early cell division and tissue formation; orientation
2. seed formation and germination
3. meristem development
4. morphogenesis (determination of final form)

VIII. MOLECULAR MECHANISMS OF PLANT DEVELOPMENT

A. use of *Arabidopsis thaliana* as a model system to study plant development
   1. member of mustard family; generally an unnamed weed (mouse-eared cress or wall cress some of its “common” names)
   2. rapid life cycle: about 5 weeks from seed-to-seed
   3. can self-fertilize (great for genetics, mutagenesis, and transformation)
   4. sequenced genome; ~26,000 genes (one of smaller dicot genomes)
   5. some call it the “fruit fly of plant research”

B. pattern formation
   1. determine location and differentiation of basic tissue types
   2. mutants with altered development used to find genes regulating development
   3. more than 50 known
   4. some broad similarities to pattern formation control in animals

C. organ formation
   1. homeotic (HOX) genes
      • similar set short, regulatory genes found in both plants and animals
      • determine expression levels of other genes that actually make the proteins used for development and structure formation
   2. well-studied HOX genes for flower development

D. hormones are important throughout development

IX. EMBRYONIC DEVELOPMENT
A. early cell division
   1. one cell from first division is small with dense cytoplasm
      • divides rapidly and repeatedly to make a ball of cells
      • becomes embryo
   2. other cell from first division is larger
      • divides rapidly and repeatedly to make an elongated structure
      • called suspensor; links embryo to nutrient tissue in seed
   3. root –shoot axis determined
      • near suspensor = future root (root meristem established)
      • other end = future shoot (shoot meristem established)

B. tissue formation from embryo ball
   1. outermost cells – epidermal cells
   2. middle layer – mostly ground tissue; also meristem
   3. innermost cells – vascular tissue

C. regulation of development
   1. plant cells differentiate where they are formed
   2. cells walls important in establishing identity (=determining development)

D. mature embryo
   1. wind up with root-shoot axis and cotyledon(s) growing out of shoot
   2. shoot apical meristem between cotyledons (may have epicotyl)
   3. epicotyl + young true leaves = plumule
   4. plumule may be encased in a protective sheath (coleoptile) – ex.: corn
   5. hypocotyl – stem axis below cotyledons
   6. root – may have clear radical, or just apical meristem and root cap

X. SEEDS AND GERMINATION
A. review of seed formation
   1. food stored in endosperm and/or cotyledons
   2. seed coat forms from integuments of ovule
      • when hardened, embryo development is arrested (dormancy)
      • hard seed coat protects embryo, keeps water out
   3. seeds are quite dry – only 5-20% water
4. seeds may last hundreds to thousands of years (seed bank in soil)

B. role of seed dormancy
   1. dormancy during unfavorable conditions – suspended animation until environment is right
   2. environmental factors (such as temp., moisture) can influence duration of dormancy – a means to sense when things are most likely to be “right”
   3. seeds protect vulnerable embryos
   4. seeds often aid in dispersal

C. mechanisms of germination
   1. seeds may need special treatments before germination is possible
      • fire (crack seed coat) – now likely in a cleared area
      • pass through animal guts – dispersed, and with fertilizer
      • **scarification** – term for physical and/or chemical abrasion of seed coats (like what happens with fires and passing through an animal’s gut)
      • **stratification** – periods of cold (even sub-zero) – helps ensure overwintering
      • variety in germination triggers within a species = better **seed bank**
   2. **imbibition** – intake of water that ends dormancy
      • dry seed rapidly takes up water when seed coat is compromised
      • embryo swells and ruptures seed coat
      • metabolism renewed (O\(_2\) required)
      • sometimes more signals are required for complete germination

D. utilization of reserves
   1. reserves in cotyledons, some other places, and in endosperm if still present
   2. include starch grains in **amyloplasts**, protein bodies, sometimes fat bodies

E. early seedling growth
   1. root usually emerges first, directed down using gravity sensor (amyloplasts in root cap)
   2. cotyledons may or may not photosynthesize
   3. seedlings are usually very vulnerable to disease and drought
   4. opening of true leaves usually considered end of early seedling growth

XI. REGULATION OF PLANT GROWTH
   A. whole plants are generally stuck where they are
B. continuous development allows plants to adapt to their environment
C. many plant cells are apparently totipotent
D. plants use hormones to regulate their growth and responses
E. environmental cues are also used to regulate plant growth and development

XII. DIFFERENTIATION
A. studied using dedifferentiated, totipotent cells
   1. proposed in 1902
   2. tested with cell culture in 1950s
      • isolate single cells
      • grow them in culture
      • callus develops
      • with right chemicals, can get differentiation (tissue culture)
B. regeneration also occurs in nature
   1. asexual reproduction
   2. cuttings
   3. generally easier to get new root system than new shoot system
   4. not all plants are equal in ease of regeneration

XIII. PLANT HORMONES
A. even small amounts will regulate physiological processes
B. control gene expression
C. transported from site of production to site of action (other cells)
D. typically produced in small amounts
E. five well-studied kinds of plant hormones:
   1. auxins (from Greek *auxein*, “to increase”)
      • basic effects
         ▪ increases plasticity of cell walls
         ▪ involved in bending of stems (promote stem elongation)
         ▪ promotes formation of adventitious roots
         ▪ inhibits leaf abscission
         ▪ promotes lateral bud dormancy
• discovery
  ▪ observed by Charles and Francis Darwin over a century ago
    i. shoots bend toward light
    ii. if a shoot tip gets no light (shaded), the shoot will not bend
    iii. shading other parts of the plant has no effect
  ▪ later experiments with removed tips showed that some diffusible substance created in the tip enhances elongation (agar block experiments)
• mode of action
  ▪ auxin causes elongation of cells
  ▪ auxin is transported away from areas in the light
• auxin and plant growth
  ▪ can cause bending within ten minutes
  ▪ also involved in fruit development
  ▪ main auxin in plants is indoleacetic acid (IAA)
  ▪ synthetic auxins
    i. used to make unfertilized fruits develop
    ii. used as herbicides (some problems: Agent Orange; 2,4-D)
• made in apical meristems, other immature areas

2. cytokinins
• modes of action
  ▪ promotes cell differentiation
  ▪ important component of coconut “milk” used in tissue culture
  ▪ works in combination with auxin to stimulate cell division
  ▪ promote growth of lateral buds into branches
  ▪ inhibit lateral root growth
  ▪ application to a yellowing leaf will keep that area green
    (promotes chloroplast development and maintenance)
• formation
  ▪ natural ones are similar to adenine
  ▪ most produced in root apical meristems and developing fruits

3. gibberellins (gibberellic acids, or GAs)
• discovery
first isolated in 1920s by Kurosawa from fungus affecting rice
- stimulated growth of rice plants
- now more than 100 natural ones known; names GA₁, GA₂, etc.

**mode of action**
- activate production of food utilization enzymes
- cause shoot elongation
- can make many dwarf plants grow
- cause biennials to bolt in first year
- hasten seed germination (substitute for cold or light)

**formation** - made in apical portions of stems and roots

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4. **ethylene**

**mode of action**
- retards growth in both root and stem systems
- hastens fruit ripening
  - i. climateric – major increase in respiration in fruits
  - ii. accompanied by a burst of ethylene production and fruit ripening
- allows abscission at fruit peduncles and leaf petioles

**formation**
- production around lateral buds stimulated by auxin
- produced in pollinated flowers and developing fruits
- released as a gas (can affect distant, unconnected plant parts)

**ecological role** – involved in promoting some defense responses to environmental stress

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5. **abscisic acid**

**modes of action**
- probably induces dormant bud formation by suppressing growth
- helps cause seed dormancy
- affects opening and closing of stomata
- application indirectly leads to leaf senescence and abscission by stimulating ethylene production
- application to a green leaf will produce a yellowed area
- some very rapid effects (thus, these not likely to be due to changes in gene expression)

**formation** – mainly in mature green leaves, fruits, and root caps
F. several others less well-understood, including **brassinosteroids** and **oligosaccharins**

G. **salicylic acid** (aspirin-like compound) is often classified as a plant hormone; involved in plant defense responses against pathogens

H. hormones and morphogenesis
   1. balances between cytokinins and auxin typically determine final plant form
   2. balances between auxin and ethylene/abscisic acid involved in senescence and abscission
   3. apical dominance (inhibition of lateral bud growth) – combined effect of auxin, cytokinins, and ethylene

XIV. ENVIRONMENTAL CUES

A. **tropisms** – growth responses to external stimuli (irreversible growth)
   1. **phototropism** – stem systems usually grow toward light; auxin involved
   2. **gravitropism** – stems grow up, roots grow down
      • stems up may be a version of phototropism (likely is)
      • root cap amyloplasts serve as gravity sensor
   3. **thigmotropism** (*thigma* is Greek for “touch”) – response to contact
      • stimulates tendrils to curl around objects; can be very rapid
      • Venus flytrap closing is actually a type of thigmotropism
   4. likely many other tropisms

B. turgor movements – reversible changes in turgor pressure
   1. typically involves active ion (usually K+) import or export, followed by water influx or efflux to relieve osmotic imbalance
   2. stomata opening/closing most obvious example
   3. also involved in “opening” and “closing” leaves and flowers
   4. may respond to various stimuli (example: sensitive plant)

C. **photoperiodism** and flowering
   1. actually a response to length of dark period
   2. plants placed into one of four categories depending on how they respond to photoperiod:
      • **long-day plants**
         ▪ flower only when day length exceeds 12-16 h
         ▪ mainly late spring and early summer
      • **short-day plants**
• flower only when day length becomes shorter than about 14 h
• mainly late summer and early fall

• intermediate-day plants
  • variety of plants respond to various other periods
  • many grasses have two photoperiods (day not too long or short)

• day-neutral plants – flower when mature and have enough food, regardless of day length

3. interrupting darkness by even a short period of light stops flowering (in short-day plants)
4. red light (660 nm) most effective at stopping flowering
5. applying far-red light (730 nm) has opposite effect
6. based on phytochrome (a blue pigment) with two states, \( P_r \) and \( P_{fr} \)
   • \( P_r \) made from amino acids
   • \( P_r + \text{photon of 660-nm light} \rightarrow P_{fr} \)
   • \( P_{fr} + \text{photon of 730-nm light} \rightarrow P_r \)
   • \( P_{fr} \rightarrow P_r \) in dark over time
   • \( P_{fr} \) is biologically active, \( P_r \) is not
   • short-day: \( P_{fr} \) represses flowering

7. searches for a clear-cut flowering hormone (florigen) have been unsuccessful
8. phytochrome also affects etiolation (pale, slender shoots for seedlings in dark) and in some species seed germination