Plant Reproduction:

Vegetative reproduction:

The process of **fragmentation**, whereby small pieces of the organism form a complete new organism is common in both lower plants and lower animals. As both plants and animals became more specialized they generally lost the capacity to reproduce by fragmentation. In some plants specialized structures are produced, such as buds, propagules, bulbils, gemmae and others. In flowering plants vegetative multiplication can take place via **cuttings** from the aerial stem, rhizome, tuber, corm, bulb, stolon, runner, leaves, or in some cases even roots. Small pieces of the structure can, through mitosis and cell division, produce an entire new plant. Such organisms produced by vegetative propagation of a single organism form **clones**. Clones are genetically similar individuals. While it is a common practice to produce clones in a laboratory or a greenhouse, some plants commonly produce clones in nature.

Sexual reproduction:

The most common form of reproduction in flowering plants is sexual reproduction. The specific nature of the process is the result of a long evolutionary history. Sexual reproduction in flowering plants is characterized by an **alternation of generations** – the **sporophyte** and the **gametophyte**. This pattern can be traced back to certain photosynthetic protists where a simple cellular alternation of generations can be found to the alternation of a one-celled stage with a multicellular stage to the alternation of two multicellular stages. Each of these is in fact two separate generations because each produces a unique product. The sporophyte produces a **spore** while the gametophyte produces a **gamete**. The way in which such products are produced and the nature of the spores and gametes differ in different groups of organisms. These differences can be characterized as gametic types (the

Figure 1 – This willow is unisexual or dioecious, producing on one plant flowers that produce only male gametophytes (pollen grains) while on a different plant flowers that produced only embryo sacs (female gametophytes).
flowering plants have oögametes) and sporic types (the flowering plants have heterospores, microspores and megaspores). Meiosis in the flowering plants is sporic, that is it occurs within a differentiated structure of the sporophyte. In addition, flowering plants may be unisexual or dioecious, a condition in which the two different gametophytes are formed on different plants, with one plant producing only microgametophytes while another plant produces only megagametophytes. Other flowering plants are bisexual or monoecious, bearing both gametophytes on the same individual.

Figure 2 – A birch tree with two different flowers (termed catkins) but both borne on the same plant. Here they are labeled “female” and “male” but such distinctions are not appropriate for the flower as it is a sporophytic structure. However, the “female catkin” will give rise to female gametophytes only while the “male catkin” will give rise to male gametophytes only. Although the flowers are separate and are thus imperfect they are borne on the same plant and thus the plant is monoecious.
The Flower:

As discussed earlier, the flower is a modified leaf and thus the anther may be thought of as being a microsporophyll (micro- small, sporo- spore bearing, phyll- leaf) containing microsporangia (spore containers) in which are found microsporocytes (small spore – producing cells). The diploid microsporocytes undergo meiosis producing microspores. The microspores develop into microgametophytes or pollen grains. The lower expanded portion of the carpel, the ovulary or ovary contains ovules. The ovules consist of several outer cell layers, the integuments, and an inner cell mass, the nucellus. The nucellus may be thought of as a megasporangium because it contains a number of diploid cells one of which will undergo meiosis ultimately forming a single functional haploid megaspore.
Figure 5 – Cross-section through an ovule showing the single megasporocyte formed within the region of the nucellus. These are all diploid cells.

Gametophyte formation:
Each microspore will undergo mitosis and in some species cell division forming a microgametophyte, the **pollen grain**. In flowering plants the pollen grain will typically consist of a single cell with two nuclei. These may or may become walled off, one from the other, by cell division. The larger of the two nuclei is called the **tube nucleus** while the smaller of the two is the **generative nucleus**. We note in
this a significant evolutionary characteristic of the flowering plants; the extreme reduction of the gametophytic generation. The single surviving megaspore will typically undergo three mitotic divisions forming an 8-nucleated embryo sac.

Figure 7 – The two-nucleated male gametophyte or pollen grain. The upper nucleus is the generative nucleus while the lower one is the tube nucleus.

Pollination:
The process of pollination brings together, ultimately, the products of the male and female gametophytes. While pollination does not ensure fertilization, pollination must occur if fertilization is to occur (in nature). By definition, pollination is the deposition of the pollen grain, by a variety of means, onto the stigma of the carpel. Thus pollination is effected by the male gametophyte. Sugar and hormones exuded by cells of the stigma stimulate the development of the pollen tube from the pollen grain. The pollen tube elongates and penetrates the stigma, continuing to elongate downward through the style and into the ovulary where it ultimately penetrates the ovule, entering through a break in the integumentary layers called the micropyle. As the pollen tube elongates, the tube nucleus and generative nucleus migrates into the pollen tube. The tube nucleus seems to have no function but the generative nucleus will divide mitotically producing two nuclei, the male gametes or sperm. In flowering plants the sperm are not flagellated. The sperm simply move along in the cytoplasm of the
pollen tube and as the tip of the pollen tube penetrates the embryo sac within the ovule it is digested dumping the two sperm into the embryo sac.

Figure 9 – Pollen grain with pollen tube. Note also the right illustration in Figure 8.

In the meantime two of the nuclei within the embryo sac (formed by the digestion of most of the nucellus tissue), one from each end, migrate to the center. These are called the **polar nuclei** and they will ultimately fuse, either prior to the entrance of the sperm or they will fuse with the sperm. The remaining three nuclei at the end of the embryo sac opposite the point of entry of the pollen tube are called the **antipodals**. They apparently have no function. Of the remaining three nuclei close by the micropyle, two are called the **synergids** while the remaining one is the **egg nucleus**.

Fertilization:
Fertilization in flowering plants is a unique process in that two fusions occur. When the two sperm arrive in the embryo sac, one migrates to and fuses with the egg. This event is fertilization. The second sperm migrates to and fuses with the two polar nuclei (or the fusion nucleus if the two have already fused). This is certainly fusion but not fertilization. The sperm migrate along a chemical gradient established by the egg and the fusion nucleus. Thus a double fusion event takes place, not a “double fertilization” as stated by a number of introductory biology texts. The fusion of egg and sperm produces the **zygote**, while the fusion of the fusion or polar nuclei and the sperm produces the **endosperm nucleus**. The endosperm nucleus divides forming a tissue unique to angiosperms, the **endosperm**.
Seed and Fruit:
The diploid embryo is contained within the embryo sac and is surrounded by cells derived from the endosperm nucleus. These cells are typically triploid (5 N in the Lily) and as they produce neither gametes nor spores they are considered by some botanists to represent a third generation unique to flowering plants. The embryo sac is contained within the ovule, which following fertilization begins to differentiate. The cells of the outer integuments become sclerenchymatous forming a hard outer covering. Nucellar tissue which still remains begins to dry out. This differentiated ovule with its developing embryo is the seed, and the hardened outer integuments form the seed coat. While these events are taking place in the ovule the ovulary is likewise differentiating. In some instances the tissues will harden, in other instances they will proliferate greatly forming a fleshy structure, in still others several different types of layers will differentiate. This differentiated ovulary is called the fruit. In some plants associated flower structures may differentiate, fusing with the ovulary in fruit formation.
Exceptional Events in Angiosperm Reproduction

Parthenogenesis
Occasionally, fertilization will not take place yet the egg will be stimulated in some way to divide. These divisions are exactly the same as those that occur in the zygote, thus an embryoid is produced that resembles the embryo in all respects except that all of its cells are haploid.

Parthenocarpy
While pollination must precede fertilization in angiosperms, pollination does not ensure fertilization. Either through naturally occurring stimuli or by artificial chemical treatment provided by humans, the ovulary may begin to differentiate even though fertilization has not occurred within its ovules. This results in the formation of a seedless or parthenocarpic fruit.

Figure 12 - Bananas are parthenocarps, the edible banana is the fruit of a sterile hybrid. The banana plant grows as a series of suckers from a rhizome. Each stem gradually droops downwards and produces at its tip the male flowers, which are sterile. The female flowers, which produce the edible fruit without fertilization, are found further along the stem. After a stem has produced a crop of fruit, it dies and is replaced by a new stem from a bud further along the rhizome. Their seedless fruit is eaten by their bat pollinators, as well as by many other animals. A banana plant may live for over 60 years.

Polyembryony
Polyembryony is an unusual event in some flowering plants, while in others such as members of the citrus family it is fairly common. It involves the formation of more than one embryo per ovule or seed. This may occur in several ways (as in animals, the cells of a 2-celled embryo may separate, each producing an embryo thus producing identical twins, 2) several sperm may enter the embryo sac simultaneously, one fusing with the egg producing a normal zygote while another fuses with one of the synergids producing a diploid nucleus that will develop into an embryoid. Thus two diploid embryos will develop within the same embryo sac but given that they were the result of different cell fusions, they would be fraternal twins, or 3) a diploid cell of the nucellus immediately surrounding the embryo
sac and at its chalazal end may somehow be stimulated to begin dividing. Again two embryos are formed within the ovule, one being the zygote and the second being an embryoid formed from vegetative diploid tissue. The result would again be fraternal twins.

Figure 13 - A seed of mango with many embryos, so-called “polyembryony” (Sriwitiwit & Suriyaapananont, 1997). One embryo may be generated by sexual reproduction, and the rest may be generated asexually by “apomixis”.

9
Plant Growth and Development

Growth
1) increase in size
2) increase in dry weight (biomass)
3) increase in the number of cells

Differentiation
An orderly series of changes that may occur with or without growth but usually accompanies growth. Differentiation leads to maturation.

Maturation
A stage of development that is typically the final state of a process of differentiation for a particular cell, tissue, or organ and is relatively long lasting. It is not necessarily a permanent state. Therefore, maturation can be characterized as follows:
- **Certain Maturity** – the final state of differentiation in which no further differentiation is possible. A cell that has reached certain maturity is a dead cell.
- **Physiological Maturity** – the usual final state of differentiation for a particular cell type, tissue or organ. It is typically a long lasting state, but as the cell is living, further differentiation is possible.

Occurrence of Growth

Where
Associated with meristems
- Apical – contributes primarily to an increase in length of an organ
- Lateral (cambia) – contributes primarily to an increase in diameter of an organ
- Intercalary - typically a transverse meristem located somewhere between the base and the apex of an organ. This type of meristem contributes primarily to an increase in length of the organ.
- Basal – located at the base of an organ and contributes to the length of the organ
- Anomalous – located other than that stated above. Most often contributes to a localized increase in diameter.

What
Cell division
What triggers it?
Perhaps critical cell size, critical cell mass, or critical cell age
Aspects
- Water uptake by the cell
- Increased plasticity of the cell wall
- Auxin mediated
- Reduces turgor pressure, thus reducing water potential
- Water osmoses into the cell creating increased turgor pressure and causing an irreversible stretching of the cell wall

Accompanied by:
- Assimilation – an increase in protoplasmic substances, vacuolar contents, and cell wall materials.

Growth Phenomena

Bases
Exogenous factors:
- Light
- Gravity
- Sound
- Electrical and/or magnetic stimulation
- Temperature
- Mechanical stimulation
- Exogenous chemicals
- Tidal and lunar influences

Endogenous factors:
- Enzymes
- Vitamins
- Hormones
- Pigments

Hormones
Organic substances produced in one cell or part of a plant and having an effect, usually at very low concentrations, on another cell or part of the plant. Unlike animal hormones that often have their effect at a site far removed from the site of synthesis, plant hormones often have their effect in cells or
tissues closely adjacent to the site of synthesis. The movement of plant hormones is most often by simple diffusion, but some may be translocated in the phloem or other cells closely adjacent to the vascular cambium.

Kinds:

Auxins

Auxins are substituted phenoxyacetic acids and include such synthetic products as 2, 4-D and 2, 4, 5-T. The typical auxin is indoleacetic acid (IAA) but a number of other compounds may be classified as auxins or produce auxin-like responses. Auxin is principally associated with elongation of the coleoptile in monocots but has a number of other effects on growth. It can stimulate stem elongation by its influence on cell elongation, is involved in differentiation, stimulates root growth, regulates fruit development, enhances apical dominance, and is involved in phototropism and gravitropism. It is synthesized in seeds and in the leaf primordia of apical buds.

Gibberellins

Gibberellins, like auxins, are acids. They are best known for their promotion of hypocotyl and stem elongation but also promote seed and bud germination, leaf growth, flowering, and the development of fruit. In addition they affect root growth and differentiation. Gibberellins are produced in the meristems of apical buds, in roots, in young leaves, and in the embryo.

Figure 14 - Structure of some synthetic auxins. Most of these synthetic auxins are used as herbicides in horticulture and agriculture. The most widely used are probably dicamba and 2,4-D, which are not subject to breakdown by the plant and are very stable.
Figure 15 – Structures of some important gibberellins.
Figure 16 – Some effects of gibberellins.

Cytokinins

Cytokinins are aminopurines. They include such compounds as zeatin and the synthetic kinetin. They are defined as compounds that induce cell division, however it has been demonstrated that they cannot do this unless auxin is also present. The source of cytokinin in the plant is debatable. Some have stated they are synthesized in the root tip and are carried upward into the stem through the xylem. Other investigators have provided evidence for the synthesis of cytokinin by a member of the methylobacteria, a group of symbiotic bacteria that live symbiotically in the roots of plants. In addition to their role in cell division, cytokinins influence differentiation, are involved with auxin in the control of apical dominance (the ability of the terminal bud to suppress the development of lateral or axillary buds), and are involved with senescence (aging). Cytokinin is thought to act through its effect on RNA synthesis.

Figure 17 – Chemical structure of the synthetic cytokinin, kinetin.
Abscisic Acid (ABA)
As its name implies, ABA is an acid. When first discovered it was called dormin because it was isolated from dormant seeds. In general, ABA is a growth inhibitor. It inhibits cell division and cell elongation, it causes stomatal closure, and together with gibberellin it is involved in seed and bud dormancy. It often works in an antagonistic fashion to auxin, cytokinin, and gibberellin.

Ethylene
The most unusual plant hormone is ethylene. Ethylene is a gas and thus for many years was not considered to be a natural plant hormone. However, it was found that plants indeed produced ethylene, particularly in response to stress. It also occurs during fruit ripening and during programmed cell death. It is high levels of ethylene in ripening fruit that causes them to eventually spoil. Ethylene is also involved in the abscission of leaves, the process that takes place each fall in deciduous plants that results in the leaves falling off.

Brassinosteroids
Possibly a new class of hormones, the brassinosteroids were isolated from Brassica pollen and found to be a steroid chemically similar to cholesterol and the sex hormones of animals. They act much like the auxins in that they induce cell division and cell elongation. Their presence in other plant groups other than the mustards has not been well documented.

Phototropism and Gravitropism
The Mechanism of Phototropism

The Darwin Experiments
Charles Darwin and his son Francis discovered the phototropic stimulus is detected at the tip of the plant.
The Darwins used grass seedlings for some of their experiments. When grass seeds germinate, the primary leaf pierces the seed coverings and the soil while protected by the **coleoptile**, a hollow, cylindrical sheath that surrounds it. Once the seedling has grown above the surface, the coleoptile stops growing and the primary leaf pierces it.

The Darwins found that the tip of the coleoptile was necessary for phototropism but that the bending takes place in the region below the tip.

If they placed an opaque cover over the tip, to occur even though the rest of the illuminated from one side.

However, when they buried the plant in that only its tip was exposed, there was no tropism - the buried coleoptile bent in light.

From these experiments, it seemed clear that

- the stimulus (light) was detected at one location (the tip)
- the response (bending) was carried out at another (the region of elongation).

This implied that the tip was, in some way, communicating with the cells of the region of elongation.

**Boysen-Jensen's Experiments**

The Danish plant physiologist Boysen-Jensen showed (in 1913) that the signal was a chemical passing down from the tip of the coleoptile.

He

- cut off the tip of the coleoptile
- covered the stump with a layer of gelatin and
- replaced the tip.

Phototropism took place normally. However, when he impervious mica between the tip and the stump, was prevented. Furthermore, this interference when the sheet of mica was inserted on the shady preparation. When a horizontal incision was made on side and the mica inserted in it, phototropism was

This suggested that the chemical signal was a stimulant as the phototropic response involves elongation on the shady side than on the side.

**The Discovery of Auxin**

F. W. Went extracted the growth stimulant.

He removed the tips of several coleoptiles of oat **sativa** seedlings. He placed these on a block of agar hours. At the end of this time, the agar block itself initiate resumption of growth of the decapitated The growth was vertical because the agar block was completely across the stump of the coleoptile and no
the plant from the side.

The unknown substance that had diffused from the agar block was named **auxin**.

The amount of auxin in coleoptile tips was far too small to be purified and analyzed chemically. Therefore, a search was made for other sources of auxin activity.

**The Avena Test - a Bioassay**

This search was aided by a technique developed by Went for determining the relative amount of auxin activity in a preparation.

The material to be assayed is incorporated into an agar block, and the block is placed on one edge of a Avena coleoptile.

As the auxin diffuses into that side of the Coleoptile, it bends away from the block.

The degree of curvature, measured after 1.5 hours in the dark, is proportional to the amount of auxin activity (e.g., number of coleoptile tips used).

The use of living tissue to determine the amount of a substance is called a **bioassay**.

The Avena test soon revealed that substances with auxin activity occur widely in nature. One of the most potent was first isolated from human urine. It was **indole-3-acetic acid (IAA)** and turned out to be the auxin actually used by plants.

Went also discovered that it is the unequal distribution of auxin that causes the bending in phototropism. When a coleoptile tip that has previously been illuminated from one side is placed on two separated agar blocks, the block on the side that had been shaded accumulates almost twice as much auxin as the block on the previously lighted side. Hence the more rapid cell elongation on the shady side of the plant.
Gravitropism of Shoots

Gravitropism also involves the unequal distribution of auxin.

When an oat coleoptile tip is placed on two separated agar blocks, as shown here, there is no difference in the auxin activity picked up by the two blocks. When the preparation is placed on its side, however, the lower block accumulates twice as much auxin activity as the upper block. Under natural conditions, this would cause greater cell elongation on the underside of the coleoptile and the plant would bend upward.

Shoots versus Roots

Unequal distribution of auxin is also the key to the

- negative phototropism and
- positive gravitropism

of roots.

The graph (based on the work of K. V. Thimann) shows the effect of auxin concentration on root and stem growth. The difference between the behavior of roots and stems lies in the difference in the sensitivity of their cells to auxin. Auxin concentrations high enough to stimulate stem growth inhibit root growth.

Possible Mechanism of Gravitropism in Roots

When a root is placed on its side,

- **Amyloplasts** (organelles containing starch grains) settle by gravity to the bottom of cells in the **root tip**.
  - The amyloplasts may be attached to **actin filaments** which are also attached to vesicles containing **PIN** proteins.
  - When inserted in the plasma membrane, PIN proteins pump **auxin** out of the cell.
  - Auxin sent down from the shoot arrives in the central tissues of the root tip.
  - Tethered to amyloplasts, PIN proteins are inserted in the plasma membrane on the underside of **pericycle** cells causing auxin
  - to accumulate on the **under** side of the root.
  - This **INHIBITS** root cell elongation.
  - So the cells at the **top** surface of the root elongate, causing the root to grow **down**.

Thigmotropism

Thigmotropism is a unidirectional response to mechanical stimulation and can be best demonstrated in the nature of vines and other climbing plants. When the stem of such a plant comes
into contact with an upright support, they will grow upward and around the structure. This takes place for two reasons. One, mechanical stimulation of the side of the stem in contact with the support apparently triggers an inactivation of the auxin on that side or a migration of the auxin to the opposite side, thus causing the cells in that region to elongate to a greater degree producing the bending effect. At the same time, elongation of the stem as a consequence of apical growth occurs first in one portion of the apex, then the adjacent one, and so on all the away around the stem apex. If this growth is viewed in time lapse photography, the tip will be seen to circumscribe a circle. This phenomenon is called **circumnutation**. Thus a climbing plant grows both up and around a support.

Nastic

May be called turgor movements and are an undirected movement – the movement is the same regardless of the direction from which the stimulus was applied.

**Thigmonasty (Thigmomorphogenesis)**

Rubbing the stems of young plants apparently triggers a series of reactions that causes cell walls to lose their plasticity. Thus auxin cannot mediate the acid growth response and cell elongation does not occur. Insectivorous plants such as the Venus Fly Trap capture their prey as the result of the insect touching consecutive trigger hairs which results in the rapid lose of turgor pressure from specialized cells along the mid-vein of the modified leaves. As these cells rapidly collapse, the two halves close around the insect. The Mimosa plant also reacts to touch with a rapid folding of the leaves and a downward bending of the petiole due to rapid loss of water from specialized hygroscopic cells. However, the Mimosa plant might be more appropriately termed **seismonastic** as the same response can be elicited by air currents or by sound waves of a certain magnitude.

Rhythmic

Cyclic movements.

**Sleep movements**
In some plants the leaves fold up at night and are unfolded during the day or the flowers close up at night and open up during the day. Such phenomena occur on a day-night cycle and are termed **diurnal rhythms**, or given that they seem to occur in a 24 hour cycle they could also be called **circadian rhythms** (from the Latin *circa*, approximately or about, and *diem* or day). The phenomena described above could be thought to be photonic in nature that is light was stimulating the opening. However, if such plants are placed in the dark, they will continue to open or close on a cycle, although the time period may not be exactly 24 hours. Initially upon putting them in the dark, when the sun comes up outside the leaves on the plant in the dark will unfold. When the sun goes down outside, the leaves on the plant in the dark will fold back up. This timing may not be exact with the conditions in nature and each day the plants are left in the dark the greater the deviation from what is occurring under natural conditions. Eventually the response will become completely unsynchronized.

**Tidal rhythms**

A particular group of diatoms grow in tubes within the sand of beaches such as those of the Chesapeake Bay. These diatoms contain several brown pigments, thus beach sand in the tidal zone will appear quite brown in color when the tide is out. That is because the diatoms come up to the surface. When the tide comes in the diatoms retreat back down into their tubes buried in the mud. An investigator from the University of Maryland dug up a portion of beach sand in the tidal zone, placed it in a bucket and brought it back to his lab in College Park. He noted that when the tide went out at the beach, the diatoms in his bucket came up to the surface and when the tide came in at the beach the diatoms went back down into the sand in his bucket. Similar to the sleep movements, these movements were not perfectly synchronized with the tide, but initially were very close. Also similar to the sleep movements, over time less synchronization was found and eventually the movement became completely unsynchronized.

**Photoperiodism**

**WHAT WE KNOW (and don't know) ABOUT PHOTOPERIODISM**

The critical factor is the length of night (uninterrupted darkness). The plant's metabolic cycles can somehow count the hours. This was confirmed by interrupting the period of darkness with a few minutes of light. Long Day—Short Night plants (treated with a flash of light to breakup a long night) will begin to flower during winter. Those plants which need Short Days and Long Night to flower may be prevented from doing so by the same procedure, fooling them by apparently resetting their counting (clock) mechanism after the flash of light.

The wavelength of the light is also critical. Red light (predominant during the day) is necessary to reset the clock which counts the hours of darkness. Far-red light will reverse the effects of red light, but has no direct effect by itself.

The chemical which detects and is changed by red or far-red light is called **phytochrome**. The form of phytochrome which absorbs red light is designated Pr, and the alternate form which is sensitive to far-red light is Pfr. The conversions between these two forms of phytochrome can be expressed by the following:

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<td>Pfr</td>
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<table>
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<td>Pfr</td>
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<tr>
<td>light</td>
<td>light</td>
<td>given time</td>
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Pr is the more stable form and slowly accumulates spontaneously during the night (or is synthesized etc.). Pfr predominates during the day since sunlight has more red light than far-red.

The test tubes in this diagram contain solutions of the two photoreversible forms of phytochrome. Absorption of red light causes the bluish Pr to change to the blue-greenish Pfr. Far-red light reverses this conversion. In most cases, it is the Pfr form of the pigment that triggers physiological responses in the plant.

Phytochrome is only an entraining mechanism, a link between the actual clock (mechanism unknown) and the hormone (yet to be discovered, but presumptively called florigen) which activates the flowering process.

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