PLANT GROWTH AND DEVELOPMENT

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Plant growth and development is accomplished through many chemical and physiological processes which are governed by environmental factors such as light, water, temperature, oxygen and carbon dioxide. Growth of a new plant usually starts with seed germination which is the sexual form of propagation. Seed stratification requirements must be satisfied. Stratification provides the conditions for pre-germination physiological maturation which occurs under specific temperature and moisture regimes. In some instances, scarification is required on seeds with hard seed coats. Scarification is the softening of hard seed coats via freezing and thawing or other physical or chemical mechanisms. When stratification, scarification and light requirements have all been satisfied, water is absorbed and the cells of the embryo begin to enlarge. This seed enlargement usually ruptures the seed coat and allows the embryonic root or radicle, to emerge. Seed is germinated when the radicle and primary shoot are visible. The absorption of water activates many enzymes in the seed that cause the breakdown of carbohydrates to the simple sugar glucose, and the breakdown of protein to amino acids. Natural plant growth regulators, called phytohornones are also synthesized and translocated to sites of action. The embryo is completely dependent upon the stored food in the cotyledons, which are the first "leaves", or food in the endosperm, which is a storage organ, until the first **true** green leaves emerge and begin active photosynthesis. Then, water and mineral uptake must actively occur through the roots. The seedling is self-sustainable at this stage providing proper environmental conditions exist.

New plants may also be started from a root or shoot piece called a cutting, which is an asexual form of propagation. Just as the germinating seedling in sexual propagation had to survive on stored nutrients and other chemical reserves in the cotyledons during the process of germination and establishment, a non-rooted hardwood cutting in asexual propagation, must also survive on stored reserves in the stems until new roots are initiated and new leaves are formed. Softwood cuttings are capable of photosynthesis during root initiation because leaves are present. Once roots have been initiated and expanded to allow water and nutrient uptake, the cuttings also become self-sustaining. The use of plant parts in this way is the easiest method for asexual or **clonal** propagation, and this process produces plants genetically identical to that from which the cutting was obtained.

Photosynthesis is the process of trapping sunlight for the conversion of carbon dioxide and water to sugar. Photosynthesis is one of the most important chemical processes on earth. It occurs in an organelle called the chloroplast that contains chlorophyll, which is the green pigment responsible for the absorption of sunlight. There are two chemical types of chlorophyll: chlorophyll A and chlorophyll B. Chlorophyll A is usually present in higher concentrations than chlorophyll B. Chlorophyll A is divided into two groups, those that capture light called antenna chlorophyll, and those directly involved in the conversion of light to chemical energy, which are called photosensitive chlorophyll. All of the chlorophyll B's are antennae pigments; none participate directly in the light conversion process.

Two other groups of pigments are found in chloroplasts. Carotenes are bright orange, or reddish when in high concentrations. The carotenes serve as antennae pigments and also are important in preventing the destruction of chlorophyll by high intensities of visible and near-visible light. Carotenoid or carotene-like pigments are also present, of which xanthophyll is the most prominent. Smaller concentrations of cytochromes or red compounds are also present.

Upon the onset of decreasing photoperiod in June and reduced day and night temperatures in September, photosynthetic and respiratory activities are reduced. Chlorophyll begins to break down faster than it is synthesized, thereby allowing the carotenes and carotenoids to become visible. The red fall colors are primarily anthocyanins which are water soluble pigments unrelated to the photosynthetic process. These pigments are synthesized at reduced temperatures when the sugars formed in photosynthesis do not move out of the leaf as rapidly as they did during the summer.

The primary product of photosynthesis is the six-carbon sugar, glucose. Other compounds such as malic and glycolic acids are also produced. All these substances are collectively called photosynthate. Glucose may be converted to the polysaccharide starch and stored in the chloroplast, or it may be transformed into the disaccharide sucrose, which is the major sugar translocated from the leaf to the stem, root, or fruit via phloem tissue.

The plant must now convert the energy stored in sucrose and starch into usable energy in the form of ATP (adenosine triphosphate) in order to synthesize protein, lipids, vitamins, alkaloids, lignin, cellulose and all the other compounds required to maintain the life of the plant, and permit its growth and development. The process by which this occurs is called cellular **aerobic respiration**.

Aerobic respiration takes place during the day and night in all living cells; it proceeds continuously in light and dark. It uses sugar and oxygen as raw materials and produces carbon dioxide and water as end products. Energy is released as a result of this reaction. It occurs in all parts of the plant. Respiration rates increase with increasing temperatures, wherein for each 10ºC increase in temperature, respiration rates double. Higher night temperatures are more critical in producing heat stress than day temperatures as carbohydrates are being consumed, but not being replaced. Respiration rates are also influenced by the stage of plant growth. Young expanding cells have a higher rate of respiration than maturing cells. Oxygen must be present for aerobic respiration to occur or the process is converted to anaerobic respiration, which is called fermentation. The result of this process is the conversion of glucose to ethyl alcohol which is toxic to most plants.

The next step in plant growth is the utilization of the photosynthetic and respiratory products. This occurs through the following major processes: cell division, cell enlargement and cell differentiation.

The most fundamental process of plant growth is the increase in the number of cells through cell division or mitosis. In mitosis, a cell divides by a regular sequence of events that ensures that each of the two resulting cells contains enough cytoplasm to maintain metabolic processes. The new cells must also contain the full genetic complement possessed by the parent cell. Active cell division occurs in the shoot and root apical meristems producing new shoots or roots resulting in increased plant height and larger root systems. Cell division also occurs in the cambium which is just under the bark. The cambium produces phloem and xylem resulting in stem diameter or caliper growth. Cell division occurs in marginal meristems which produce leaves; it occurs in fruit, and it occurs in adventitious bud and root formation.

All plant growth that involves an increase in the number of cells is the result of an active meristem. A meristem is a small group of cells that remain non-specialized or non-differentiated, and they retain the capacity for rapid cell division.

The main meristematic areas within the plant are the apical meristems of the terminal and lateral shoots, the vascular cambium, the root apex, and the marginal meristems active during the growth of leaves. Leaves of grasses, lilies, and other monocots have regions of cell growth at the base of their leaves. These regions are called intercalary meristems and they provide new growth unless they are dormant. Thus, grass leaves continue to grow from the base, which is why lawns require periodic cutting. If these leaves grew from apical or marginal meristems, they would cease to grow once cut.

The vascular cambium is the meristematic tissue located between the xylem and phloem of woody plants. In addition to its effects on increasing the diameter of the tree trunk by wood production, the cambium is also responsible for wound closure. When a wound is made in the bark of a tree or when a branch is cut off, the vascular cambium in the area of the wound is triggered into rapid growth. This meristem produces the callus which eventually grows over to close the wound.

The second stage of plant growth is called cell enlargement. This involves growth in size which is driven by the absorption of water into the cell. Cells may enlarge in all dimensions to become essentially spherical, but normally the enlargement will be directional resulting in an increase in length called elongation, or an increase in girth. Much of the increase in young root and shoot length is due to cell elongation. Cell enlargement in girth results in increased caliper.

The third stage of plant development is cell differentiation. This is a change in either the structure or function of a group of cells to form plant organs. A cell that develops chloroplasts can photosynthesize and is both structurally and functionally changed. Cells of the xylem are functional in moving water only after they have formed secondary walls and have died.

The processes of division, enlargement and differentiation must be precisely regulated and controlled to provide the typical structures and functions required for plant growth. Photosynthesis and respiration supply the energy and chemical compounds needed for plant growth. Water and nutrients, proper temperature, genetic regulation and many metabolic activities are involved. Specific chemicals that regulate plant growth are also involved. The **natural** forms of these compounds are called plant **hormones**. Plant hormones are organic compounds made by the plant; they are effective in very small quantities, and they move from the site of production to the site of action, i.e. a cell, tissue, or organ. There are five major groups of the classical plant hormones: auxins, gibberellins, cytokinins, ethylene, and abscisic acid (ABA). More recently discovered plant hormones include brassinosteroids, systemin, jasmonie acid and salicylic acid. Only the plant-produced forms of all of these compounds are called hormones; the man-made or **synthetic** forms of these compounds are called **growth regulators**.

Auxins have been found to be the main plant hormone responsible for apical dominance, wherein the apical meristem of an actively growing shoot suppresses the growth of lateral buds. When the stem apex is cut or "pinched" off, lateral buds below the apex begin active growth. Removal of the stem apex removes the supply of auxin in the stem, and this lowered auxin production releases the lateral buds from apical dominance. This phenomenon explains, in part, why horticulturists prune the top of a plant in order to force lateral branching. In some cases the lateral bud closest to the cut may grow so much faster than the others that it becomes dominant and again completely suppresses the other buds below it. In this case only one "break" would occur at any given cut. The number of "breaks" per cut is quite variable among different species.
Auxins are also instrumental in the initiation of roots from stem cuttings. Indoleacetic acid (IAA) is the **natural plant hormone** that promotes rooting. Indolebutyric acid (IBA) is the **synthetic growth regulator** that promotes rooting.

Gibberellin or gibberellic acid also has dramatic effects on plant growth. Gibberellin functions primarily in promoting cell enlargement. Some dwarf plants have been shown to be dwarfed because they cannot produce their own gibberellins. The “bolting” response or the rapid elongation of the flower stalk of cabbage, spinach, and some biennial herbaceous plants has been shown to result from a rapid increase in the gibberellin content of the stem. In addition to gibberellin effects on cell enlargement, this class of hormones has also been shown to stimulate seed germination. Soaking seeds in a gibberellin-containing solution dramatically increases the rate and percentage of seed germination for many species. In some species, gibberellin is also effective in breaking bud dormancy. The several forms of gibberellic acid (Gibberellins) have wide commercial uses, from increasing the rachis length of grapes which produces more open bunches, to the improvement of the malting process of barley.

Cytokinins are produced in the root system and translocated to the shoot portion of the plant. These hormones promote cell division, aid in the regulation of stomatal closure, and may prevent senescence or aging of some plant parts.

Other plant hormones behave as inhibitors rather than promoters of growth. Two of these inhibitors are abscisic acid and ethylene. Abscisic acid (ABA) is involved in the abscission of leaves, fruits and flowers; in maintaining the dormancy of buds and seeds; and in inhibiting other growth responses. Ethylene is produced by ripening fruits such as apples. It rapidly increases the rate of ripening or senescence within the plant. Ethylene is a gaseous compound and can trigger green bananas to ripen, and can also have severely damaging effects on cut flowers such as carnations and roses. For this reason, flowers and ripe fruits should never be stored in the same refrigerated storage, as the vase life of the flowers will be severely limited. Ethylene also provides beneficial effects in that it promotes flowering of bromeliads and may be used to hasten the removal of leaves from nut trees and cotton plants. Ethylene is also used for early defoliation of some nursery crops to facilitate machine harvesting and improve storability. Ethylene also can be applied to tomatoes to increase the uniformity of ripening.

Over the last 15 years, new information has pointed to additional plant hormone regulated systems. The brassinosteroids play a very important role in directing the change that occurs between the growth of plants in the dark and the development that occurs in the light. When a seed germinates underground, the seedling remains non-green and rapidly elongates. In dicots, the hypocotyls remains hooked over to protect the cotyledons during soil penetration. A similar growth habit occurs in the dark, as can be seen when purchasing bean sprouts in the local supermarket. This growth is known as etiolation and is controlled by the action of the plant hormone brassinosteroid. Plants that are unable to make brassinosteroids lack the ability to develop the characteristics of etiolated growth and have difficulty emerging from the soil after germination.

Systemin, jasmonic acid and salicylic acid are all involved in the response of plants to physical or biological stress. Systemin is a small, 18-amino acid peptide that moves through the phloem to signal the plant by systemic whole plant alterations in gene expression, to respond to localized wounding. Similarly, jasmonic acid induces global responses to a variety of stresses. Interestingly, the methyl ester of jasmonic acid is volatile and as a vapor can signal wounding and stress responses in plants nearby the one that received the injury or initial stressful event.

Plants frequently restrict the spread of fungal bacterial or viral pathogens to a small zone around the site of initial infection by forming a necrotic lesion as a result of localized cell death known as the hypersensitive response. Salicylic acid appears to be important in the initial development of the hypersensitive response as well as the systemic, whole plant, response to biological infections.

All plant hormones have in common the following three factors: they are produced naturally by the plant, they are active in very minute concentrations, and they are translocated within the plant from the site of production to the site of utilization. They are all very critical to proper plant growth.

Environmental factors also play a key role in plant growth and development. The qualitative and quantitative modifications of growth by light, water, temperature and nutrients are critical to profitable nursery and landscape management. The interaction of environmental factors, physical and chemical reactions, and genetic constitution, determines the limits and degree of plant response. Plants under long-term water stress or plants that receive inadequate nutrition will be less vigorous and may bear abnormal leaves, flowers, or fruit. If an environmental stress occurs for even a short time at a critical stage in development, the plant may never express its full genetic potential.

The genetic and environmental interaction of each plant species determines the survivability and worldwide distribution of that species. The growth-promotive and growth-inhibitive periods that occur in a plant's annual life cycle are based on this interaction. This cycle of growth promotion and inhibition for survival purposes is shown in Figure 1. Although the active growth period is extremely important for increasing plant size, this growth period is also involved in preparation or acclimation for winter hardiness and dormancy. Without such acclimation, plants would not survive the climatic conditions of the northern hemisphere. Refer to the chapter on Plant Cold Hardiness and the chapter Winter Protection for additional information.

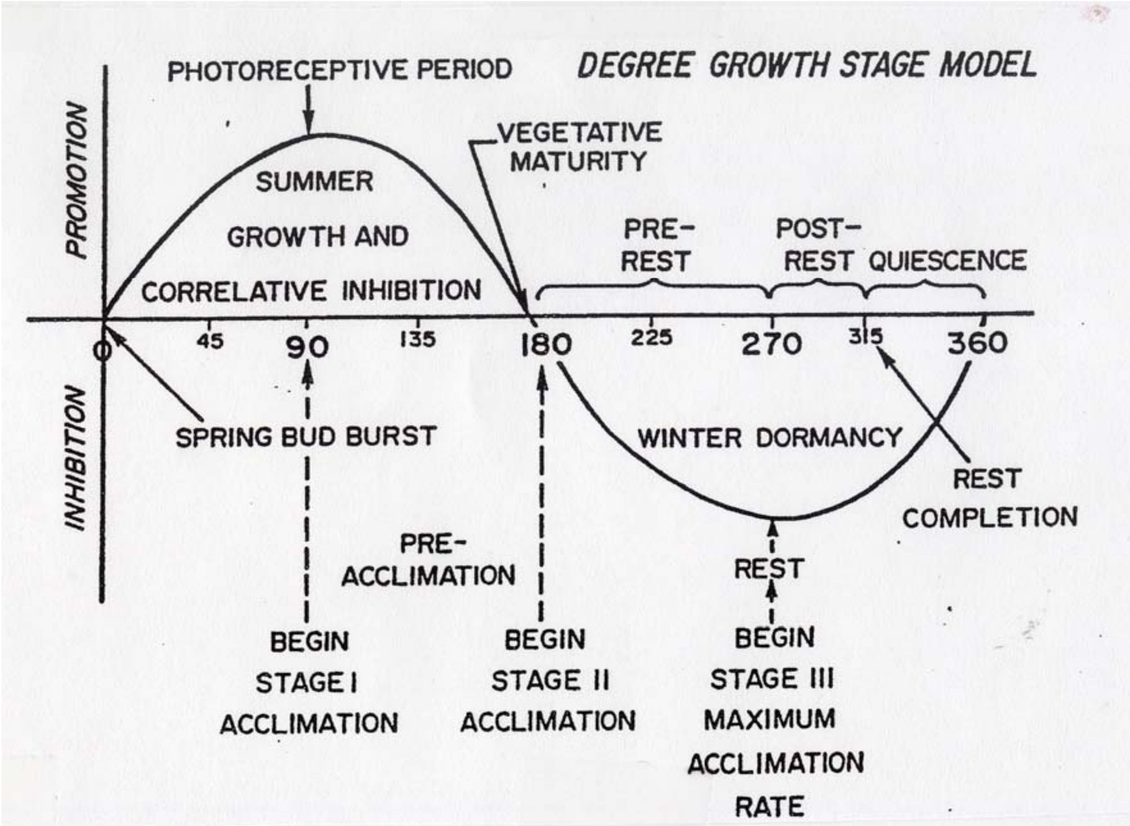

Figure 1. Degree Growth Stage Model showing the timing for active growth and rest period. (From: Fujigama, L. 1985. Degree Growth Stage Model.)