Herbicide Actions

by Tim Braun

Weeds have been evolving into a strong pest for over four hundred million years and in order to farm and produce crops needed for basic nutrition weed control has become a way of life for crop producers. For the last seventy years or so herbicides have become the main means of weed control. Other methods of weed control are still used in agriculture along with chemicals. Organic forms of producing crops are required to use methods of weed control that do not include chemical forms of herbicides. The costs of producing crops needed to feed the ever increasing populations of humans and the shortage of labor leads to the use of herbicides to control the weeds that have survived the natural changes in the earth's environment. In order for humans to produce food and clothing the competition with weeds for the space and resources needed for the growing of crops and animals used as food has become a biological combat.

The research that has allowed growers to control the weed plants without hurting the crop plants, humans and other animals that consume them has resulted in several approved and successful herbicides. These herbicides are discussed here on what the plant organism is plus a description or the herbicide and what its mode of action is when controlling the weed. Trade names are used, but the basic chemical names are added because of the many duplicate names used by the makers of these herbicides.

Growth Regulators

In nineteen forty one the herbicide, 2-4D was co-discovered by two teams of researchers in two different countries. In the United States the research team was "Templeman and Colleagues at "ICI" (USA) and in England research was done at "Nutman and Collaborators at Rathamsted Experimental Station" (UK). If the research was done for agricultural purposes it could be done in spite of the fact the countries had signed the Geneva Protocol as well as other needed treaties. At Rothamsted some agricultural products were actually discovered that increased agricultural crop yields. 2-4D was developed, but it wasn't used until after the second world war in nineteen forty six. 2-4D was the first known successful *selective herbicide*. 2-4D became a winner and did a great job of weed control in cereal grass crops like wheat, corn and rice. It killed dicotyledon weeds or the broadleaf weeds and left the monocot leafed crops like wheat.

Over fifteen hundred herbicides now contain 2-4D. It has been one of the most intensely studied herbicides on the market. Bacteria breaks down the chemical in soil. The half life of the chemical was found to be in a period of one and a half to sixteen days. It does not appear to be broken down by sunlight. 2-4D is one of the most studied herbicides by health officials and studies to determine dangers of 2-4D to the environment continue to this day. It is one of the most tested herbicides for its safety and testing has shown that it is safe, but restrictions on its use are still being enforced. As late as August eighth of two thousand and seven the Environmental Protection Agency issued a ruling that stated "existing data does not support a link between human cancer and 2-4D exposure".

This herbicide is usually sold in products mixed with other herbicides to increase the control and to prevent the increase of weeds that are resistant to control by 2-4D. These weeds if not controlled become immune to it. One of the other herbicides that was mixed with 2-4D was a chemical with similar properties called 2-45T. This formulation called "Agent Orange" was used in the Vietnam War to expose enemy locations by killing the jungle vegetation.

When I was at the University of California at Davis in nineteen fifty seven I worked in the plant physiology department where two of us ran studies using 2-4D mixed with 2-45T that had the radio active carbon as a part of their chemical make-up. We applied this mix to the leafs and other parts of bean plants. Then we would let them grow for different lengths of time to allow the chemical to spread through the growing plants. We applied gyberillic acid to the plant so many days before, then at the same time as the weed killer and then after the weed killer was applied. Our research was to see if the gybberillic acid would speed up the activity of the herbicide mix. The forest service was using this combination in the mountains above Sacramento, California for the blister rust disease control.

After we dug up the treated bean plants we washed them and dried them with paper towels and immediately froze them with dry ice. Then we laid them on photographic paper. The radio active carbon in the weed killer would make a picture of its travels through the bean plant. The results were very definite that gibberillic acid would speed up the spread of "Agent Orange" through the bean pants. We both had to be checked at the clinic for cancer once a month. The doctors checked us down our throats and up our rear ends. We were alright. Years later in the cotton fields of Kern County I did some tests using zinc applications after the application of gybberillic acid to the cotton leaves and these tests proved that the acid increased the activity of the zinc resulting in increased yields.

The herbicide 2-4D is a synthetic plant hormone called an auxin. It's a Greek word meaning to grow or increase. The growing plant hasn't been found to have a nervous system like animals that have a brain and nerves, but plants do have a system that reacts to the surrounding environment with the movement and activity of the plant's auxins. Plant parts are made up of cells that form body parts: leaves, stems, roots etc…. In the living plant the auxin hormones work with or against the other plant hormones depending on the changing conditions around the plant.

In nature there are said to be four natural auxins in plants. These include: (these are chemicals and this is how they are written) No. (1) is indole-e-acetic acid or IAA and this auxin is the main auxin in plants; Number (2) is the 4-chloroindole-3-acetic acid; (3) phenylacetic acid; and (4) the indole-butyric acid. The main one, IAA, is the most important auxin of the four. Because these natural auxins break down when not in live plants scientists are not able to reproduce these auxins in a stable condition like the 2-4D and 2-45T.

The auxins are stimulated to act by the changes in the environment around the growing plant and by direct messages from certain genes located in the DNA in the nucleus of the plant cells. The messages are sent from established cells to the growing cells by the auxin molecules that are formed by the ribosomes in the cells (where molecules like proteins are made under the direction of the gene message sent from the DNA inside the nucleus of plant cells). Auxines can be produced in all plant cells, but the production doesn't occur until the cell is stimulated to do so; therefore the auxins must travel throughout the plant from their site of production to where they do their job. The auxin travels through the plant in the phloem tubes of the living cell vascular system. Auxins travel with fluids in the phloem moving from the food making or storage areas of the plant's body to the area in the plant where it is used for growth or where it is again stored.

Auxins can also travel through the plant by going from cell to cell through the cell's membranes by diffusion (higher concentration to a lower concentration). The plant cells also have what are called infflux transporters. These are proteins that are in the cell membrane that can allow the plants auxins to move **into** the cell's membranes. They are located at the top and the bottom of the cell and at the sides or lateral surface that allow auxins to move from the cells where they were produced to areas where new cell growth is needed. The plant also has efflux transporters on their membranes that allow auxins to move **out** of the cell. Only auxins that have been made by the plant are able to move through these efflux transporters. The synthetic auxins that are made to use as herbicides can enter cells in the plant through the infflux transportter , but it is said that these synthetic auxins like 2,4-D cannot leave the cell that they have entered by efflux transporters. 2-4D start causing critical changes to the living cells. The plant is harmed and eventually dies.

Auxins coordinate the development of the entire plant. This starts with the cells. Then they move to the tissues and then the entire plant. The auxin molecules have the ability to start plant responses on a direct basis by stimulation or by inhibiting the expression of certain genes. In some cases by methods other than gene expression. Meristem cells are undifferentiated. Until meristem cells are activated they have no set purpose in the plant except for growth. (Meristem cells double themselves resulting in plant growth.) Auxins activate them. The cells start growing into the particular kind of cell needed for the growth of the plant. The cell becomes differentiated.

Plant organs get their shape by auxin activities. This results in the final shape of the entire plant. In the embryo at the very start of the plant's growth the future body's auxins decide what the future shape of the plant will have throughout its lifetime. Without this direction the plant would be a group of cells of the same size with no purpose. In the embryo the formation guided by the auxins develops the new plant body with directional poles for growth. At this very early stage the buds of future organs are formed. Auxins coordinate the development of these plant organs which include: roots, leaves and all the other future plant parts.

Auxin is able to control where it travels throughout the plant because of its position where it is produced. One of the vital locations of auxin production is in the apical bud of the plant, the growing tip at the top of the plant. This allows the auxin to be transported down and it therefore can inhibit the growth of lower, lateral buds. Otherwise the lower buds would compete with the top bud. This auxin activity gives a shape to the plant that allows all the leaves to receive sunlight that provides energy for the photosynthesis to produce food for the plant. The auxin produced by the apical bud provides a dominance to the bud and this is called "apical dominance". Auxin doesn't act alone in its act of limiting the growth of the lower part of the plant. Other plant hormomes like the cytokinins interact with the auxins to control this growth.

I planted a citrus hedge in my back yard that needs to be trimmed constantly. The objective is to form a box hedge. The amount of auxin going to the roots from the stems decreases because trimming increases the side growth. This increase in side growth decreases the amount of root growth because the auxins are going to the side growth. This lack of root growth provides more nutrients for the very top growth; then I'm constantly trimming the top growth when it begins growing faster. I have four types of citrus in the hedge and the lemons are giving me the most new growth trouble.

Another visible sign of the presence of Auxins is that they will collect on the side of the plant not receiving light. That side of the plant will start growing faster than the side with high amounts of light. The plant body then will grow longer cells and start leaning toward the high light side of the plant. This is named "phototropism". Gravity also causes an auxin response in plants. Gravity causes the auxin to trigger directional growth. Stems will grow up away from the pull of gravity and roots will grow down due to the pull of gravity. Potatoes when laid down in storage will give out one bud and several roots. If the potato is cut up the potato will produce a bud and roots for every piece of potato. The buds grow up and the roots grow down.

Lipid Inhibitor Herbicides

Over four hundred and fifty million years ago when plants moved from their home in the water to become land plants one of the main parts of their body that they had to change was their skin. In order to keep the vital water inside their bodies when they were no longer submerged in water they had to grow a substance the could keep the fluids inside their bodies. They grew a waxy material called cuticle. This kept the air outside their skin from evaporating the liquids that were inside their bodies.

Lipids consist of a great many compounds containing fat and other chemicals that do not dissolve in water, but they also contain many other compounds that have nothing to do with fatty acids. Lipids are the main material that make up the plants membranes. These membranes contain the nucleus inside of the plant cell where the DNA on chomosomes and other vital cell parts are located. This membrane inside the plant cells isolates the chromosomes from the cytoplasm in the cell. The cell membrane along with the cell wall contain the cell parts of plants. Lipids contain fats which are a chemical reserve of free energy needed by the plant to operate. Some of the lipid derivatives act as plant hormones and secondary messenger compounds. Lipids have a great deal to do with signal pathways in the plant's body. Liquid lipids are oils and solid lipids are fat. The lipids that are wax are in the plant cuticle.

Lipids are produced in a series of reactions where enzymes are involved. There are several specific enzyme called fatty acid synthase that carry out the conversion of amino acids to the needed fatty acids or lipids. Inhibitions of the fatty acid synthesis pathway to production of lipids results in the halt of membrane formation, chloroplast formation and multiplication thus causing a halt to cell membrane formation and cell division.

There are two families of synthetic herbicides that inhibit the specific enzyme that is responsible for the making of these vital lipids. These inhibitors only work on grasses and not on broadleaves, because the specific needed enzymes are not found in broadleaf weeds. Weed killers or herbicides that are lipid inhibitors are called (fops) and (dims). The name (fops) is for Aryloxyphenoxys that changes from an ester to an acid that inhibits the key enzyme needed for the plant manufacturing of the lipid. Hoechst AG is the company that developed this chemical in nineteen eighty. The company, Hoechst AG merged with Rhone Poulenc in December nineteen ninety nine to form the company Aventis.

The (fops) include: diclofop-methyl, **Hoelon**; fenoxaprop-P-ethyl **Acclaim,** and several others; fluazifop-P-butyl **Fusilade**; and quizalofop-P-ethyl **Assure II**. Hoelon can be used on grass crops, wheat and barley. Acclaim and others that are fenoxaprop-P-ethyls can be used in cool-season perennial turf grasses because they have reduced activity on this cool-season crop. Acclaim can also be used on soybean, rice, trees, ornamentals, and conservation reserves. Fusilade can be applied to several broadleaf crops which include: soybean, cotton, asparagus, carrots, onions, garlic, sweet potatoes, and some vegetables and tree fruits. Assure is applied to several broadleaf crops that include: soybean, cotton, pulse crops, mint, sugarbeets and noncropland areas. (Always follow label directions. Labels change.)

These lipid inhibitors are all applied to the foliage. They are systemic and translocated in the plant to the meristem cells. Hoelon and Acclaim do not control perennial grasses because they are not as mobile and do not travel throughout the plant as the other (fops) do. All of these herbicides will have failures of control on some weeds that are resistant to the particular herbicide. If they enter the soil these herbicides will be broken down by bacteria. Assure II takes sixty days to break down and the rest of them are broken down in thirty days.

The symptoms for damage to the weeds and other susceptible plants include: dead and rotting tissue in the meristem cell areas of grasses. The death is slow. The growing points and inner whorl of leaves (meristem locations) start dying in a few days. The outer leaves remain healthy for several days but eventually die.

Cyclohexanediones (Dims)

These herbicides inhibit lipid production by the plant by tying up the enzyme, (ACCase) acetyl CoA carboxylase. (Dims) do not have to be formulated as an ester formulation as the (Fops) do. Their activity is similar to the (Fops). (Dims) were formulated and developed during the nineteen eighties with the same activity as the (Fops) herbicides. Clethodim is **Select or Prism**; Sethozydim is **Poast**; and tralkoxydim is **Achieve**.

Select or Prism is used on crops that are broadleaf and include: soybean, cotton, sugar beet, onion, garlic, tomato, alfalfa, peanuts, dry beans and non-bearing food crops. It is used in fallow and in non cropland areas. Poast is used for weed control on soybean, canola, cotton, flax, mint, peanuts, sugar beets, fruit crops, sunflower, forage legumes, vegetable crops, herbaceous and woody ornamentals, forest nurseries and Christmas trees. Achieve is used on grass crops, wheat and barley.

These herbicides are applied to the leaves. They are absorbed and transferred to the meristem cells of the plant. They kill annual and perennial grasses. They inhibit a form of enzyme (ACCase) that is in grasses and not in broadleaf plants. They break down by microbial action. They do not last long in soils where they have a half life of three to five days.

The symptoms of their activity as herbicides include: dead and rotten tissue in the meristems. Growth stops right away. The growing point and inner whorl of leaves dies after a couple of days while the outer leaves stay healthy for several days before they die. Older leaves may turn purple, orange or red before chlorosis occurs. If these herbicides are applied preplant the plants that emerge from the treated soil may have root growth problems and leaves will fail to emerge out of the seed cover.

Soil Applied Lipid Inhibitors.

Discovered in nineteen fifty seven by the company, Stauffer, and sold under the name, Eptam and Eradicane, was a chemical called thiocarbamate. This herbicide inhibited the enzymes, elongase, and not the enzyme, ACCase. It contained sulfur in place of the hydroxyl O of carbamic acid. Other brand names included: Sutan, Ro-Neet, Ordam, Bolero/Abolish, Avadex/Fargo and Tillam/Edge. The chemical acts on shoots by inhibiting the production of suberin, a long chain fatty acid. This causes dehydration. Suberin is in the group of lipids that are waxes and cutin. Seedlings are not able to emerge from the soil. Broadleaves that do emerge from the soil have cupped, puckered, or crinkled leaves and thick cuticles, because the cuticle waxes of the leaves are not formed naturally.

The roots and coleoptiles (seed leaves) of grass seedlings absorb this herbicide; therefore the herbicide must be incorporated. We used to apply Eptam to growing alfalfa fields through the irrigation system. Other growing crops include: clover, beans, flax, potatoes, sugarbeets, citrus, cotton, safflower, walnuts, almonds, tomatoes and sweet potatoes.

Photosynthesis Inhibitors

Energy in the form of light from the sun is used by growing plants or weeds to change carbon dioxide in the air along with water to glucose and oxygen. The sun provides this light energy and plants use only a small percentage of this energy. Seventy five to eighty five percent of the sun's energy is used to evaporate water; five to ten percent goes into the soil as heat storage; five to ten percent goes into heat exchange with the atmosphere by convection and only one to five percent goes into photosynthesis.

The energy in light is made up of small units of energy. These units are called photons. In the plant leaf and stems there are cells that can capture the energy of these photons. These cells have chloroplasts in them that are able to capture the light from the sun or these photons and through the process named photosynthesis the sunlight energy is combined with water and carbon dioxide from the air to form physical carbohydrates and oxygen. The chloroplasts are inside the plant cell that has a nucleus with DNA and a vacuole that have their own membrane confining them. The chloroplasts also have a double membrane confining them. Inside the chloroplasts' are other membrane covered organisms named: thylakoids. These thylakoids make up different regions in the chloroplast. The thylakoids are disk shaped with fluid inside them called lumen. Some of the thylakoid disks are in stacks pressed together and they are called “grana”. The other thylakoids are not in stacks and they are completely exposed to the liquid in the chloroplast and this liquid is called “stroma”. All of the thylakoids are connected together and the fluid in them “lumen” flows through all of them.

The thylakoids contain two systems in them. One system is called “Photosystem I” and the other system is called “Photosystem II”. Photosystem I is found in the unstacked membranes that are fully exposed to the fluid in the chloroplast called stroma and Photosystem II is found in the stacked membranes called the grana membranes. Both of these systems function in the first part of changing light energy into chemical energy.

These systems have equipment including antenna to absorb the light, and pigments for accepting light energy then they transfer it to reaction centers where it is converted to stable chemical products.

<u>How sunlight energy is captured by the plant</u>.

The molecules of the chloroplast have electrons moving in orbits in the molecule at a stable speed caused by their lowest level of energy. The energy they need is just enough to keep them in orbit. When a photon with energy from the sunlight hits one of these chloroplast electrons the electron gains energy that puts it in a higher orbit. In order to get back to its normal orbit the electron will release energy. This energy can also be lost in the form of heat or light. The molecule, that the electron released its excess energy to, can also donate this energy to other molecules. Molecules try to stay in one energy level while in orbit.

Green plant cells have chloroplasts that have several molecules that will accept the excess energy. These molecules are named phaeophytin, quinone, plastoquinone, cytochrom bf, and ferredoxin. These molecules form a chain of molecules where the electron energy passes from one molecule to the other molecules in the chain.

This chain of reactions goes through both photosystems. The action begins in photosystem II and transfers to photosystem I. This energy can be transferred to any of the chloroplast molecules, thus ‘exciting them‘. When a chloroplast molecule loses an electron the electron may be lost to an electron-acceptor molecule. This is called “a charge separation event“. The excited pigment reduces the accepting molecule. This activity converts light energy to chemical products and this is the main result of photosynthesis.

The electro transporting chain of molecules in the thylakoids moves electrons from the water that is in the liquid lumen inside the membranes of the thylakoid to active compounds in the liquid part of the chloroplast called the stroma of the chloroplast. These active compounds in the liquid stroma include nicotinamide adenine dinucleotide phosphate or (NAPD). The light energy splits water molecules into hydrogen protons (H+) and oxygen (O2). The (H+) makes the liquid lumin in the thylakoid <u>acidic</u>. This adds a hydrogen (H+) to the (NAPD) forming the (nicotinamide adenine dinucleotide phosphate hydrogen) or NAPDH. This NAPDH is one of the most powerful accepters of electrons and suppliers of hydrogen ions known in biological systems. At the same time the adenosine diphosphate, ADP, is phosphoralated adding a phosphate to adenosine **tri**phosphate, ATP. This allows the chemical to undergo even more chemical reactions.

The ATP and NADPH are used by the plant to change carbon dioxide to other plant organic molecules called carbohydrates. Photosynthesis uses all three: energy collection from the sun, water from the soil and carbon dioxide from the air to manufacture needed plant organic molecules. At the same time oxygen is released to the atmosphere for the respiration needs of plants and animals.

Photosynthesis inhibitors do their damage by breaking up the chain of activity of the electron. The inhibitors divert the electrons from the reaction chain to the rest of the plant cell. The loose energy ends up destroying the plant cell. If this is a weed the inhibitor becomes a herbicide.

The electron moves through the photosystem II to photosystem I. One of the inhibitors, triazin, works on the last part of the molecule chain in photosystem II which is a very vital spot. Other inhibitors called the bipyridillium tie up the molecules on the last part of the chain at the end of photosystem I. These herbicides are oxidized by accepting electrons that produce superoxide radicals that damage the photosynthetic processes of the plant.

The triazines include Simazine which was released in nineteen fifty six by Ciba Geigy Corporation. They block the electron transport system in phtosynthesis by connecting to sites of the of the protein called quinone. The membranes of the plant are destroyed by the released electrons.

Atrrazine another similar inhibitor of photosynthesis was released in nineteen fifty eight. It became one of the most popular herbicides of field corn. This class of herbicides include: Ametryn named Evik. It's used in corn, banana, pineapple and noncrop area; Atrazine called Aatrex is used on corn and grain sorghum. It is used in warm season grass. Velpar or hexazinone in used on general vegetation which includes shrubs and trees. It is used in forest crops because it is selective on conifers. Sencor and Lexone or metribuzin is used for weed control in alfalfa, asparagus, carrots, field corn, Potato, pulse crops, small grains, soybeans, sugarcane and tomato. Simazine or Princep is also used on corn and other crops including fruit and nut crops or trees, Christmas trees and nursery crops.

The transportation of these inhibitors through the plant is in the xylem therefore. It is a systemic. It is used preplant, preemerge and early post emerge. Those that have good water solubility can be foliar applied. This is an annual broadleaf weed herbicide, but it will suppress some annual grasses. Some plants have different sequences of the amino acid residues and this can cause different effects with the same herbicide. There are also plants that have their own detoxification systems for herbicides. Corn is insensitive to Atrazine because of the corn's glutathione, a detoxine. This chemical is inactivated when taken into the cell vacuole storage site where it is harmless.

When applied in sandy soils this herbicide is more available because of less adsorption to clay content. Organic soils produce more organisms that break down the herbicide. High pH allows the chemical to last longer and stay active for a longer period of time. In low pH soils the herbicide breaks down at a faster rate. Hydrolysis will break down this herbicide reducing its reactive period of time.

Triazine activity is longer and greater in dry soils, cold soils, low organic matter, low clay content and high pH soils. Carry over of the active part of the chemical can be a problem. The crops that are harmed by Atrazine include oats, small-seeded legumes, sugarbeets and vegetable crops and these crops should not be planted for a period of two years after application.

Leaching in most soils is not a problem because of the strong affinity that Atrazine has for clays. Atrazine has been found in groundwater. For this reason Atrazine has been restricted by law in some cases. Shallow water tables and sandy soils are most prone to leaching of Atrazine. Some surface waters have amounts of Atrazine that cause troubles. With the good water solubility and the half life there should not be a problem. One of the problems, though, is the wide use of Atrazine especially in the north central part of the United States. Atrazine can move into surface waters while it is attached to soil particles when the soil particles move into the water table. When it moves into anaerobic areas of the soil, Atrazine can have a half life of two years. (No air to activate bacterial breakdown). In fields, that have water that is poorly aerated at the soil surface and that contains sediment from crop fields, Atrazine contamination has become a problem.

Once a plant that is mature enough to begin photosynthesis it will start to show injury symptoms. The leaf margins start to yellow. The yellowing appears after cotyledons and true leaves are visible. The yellowing is on leaf tips and between the leaf veins. Then the leaf tissue becomes necrotic (dead spots or whole areas of dead tissue). The larger and older leaves show symptoms first. The necrosis moves from the margins and tips to the leaf center and base of the leaf. The injury is greater on soils with a pH over seven point two.

Basagran, Benzothiadiazinone, was released by the company, BASF, in nineteen sixty eight and became the first good chemical to control cockleburs in soybeans. It's applied to the leaves and needs very complete coverage to be affective. Basagran controls broadleaf weeds and sedges in large seed legume and grass crops. Crops on the label include beans, peanuts, peas, corn, rice, sorghum, soybean, pepperment and spearment.

Basagran controls cocklebur, ragweeds, smartweeds and sunflower.

It does a good job with excellent kill on cocklebur, smartweed and ragweed with good kill on velvetleaf , nutsedge, sunflower, and jumsonweed.. Grass weeds are tolerant to Basagran applications and lambsquarters and pigweed receive poor kills.

Basagran has a half life in the soil of twenty days. It is rapidly broken down by microbes in the soil. The symptoms include: chlorosis and necrosis in the foliage that receives the spray. On older leaves necrosis is coppery. The plant will be stunted. It takes three days for symptoms to appear. The crop that is sprayed may show some speckling or bronzing, but the crop plants generally outgrow the injury within ten days or less.

Buctril, Brominal, Bronate and others have the common name bromoxynil and ioxynil with various unlisted trade names. In the year of nineteen sixty three bromoxynil and ioxynil were released by the chemical company, Rhone Poulenc (it is now called Aventis). This was after Hoescht AG merged with Aventis. Buctril is an inhibitor of photosynthesis by binding to the quinine protein in the chain that is located in the photosystem II at the end of the chain before sunlight activated electrons are passed into the photosystem I chain of proteins. This activity diverts electrons from the normal chain and these diverted electrons destroy the plants immediate necessary membranes causing injury and death of the plant or weed.

Buctril is applied to the foliage of the target weed. It is a contact herbicide applied post emergence. This weed killer affects broad leaf weeds.

It is most affective on annuals including: nightshade, mustards and smartweeds. The weeds that are best controlled by Buctril are the weeds that retain the spray the longest. This allows for a higher uptake of the herbicide. Grass plants are generally tolerant to Buctril applications.

This class or herbicides are bound to or absorbed by the soil not allowing them to reach the weed roots. Soil microorganisms rapidly consume and breakdown these herbicides. The half life in soils is seven days.

Target plants treated with these herbicides which include Buctril cause a rapid necrosis of the sprayed plant parts. The resulting injury of this herbicide is confined to the foliage that has this material applied to it.

With the common name diquat (trade name: Reward and others) and with the common name paraquat (trade names Cyclone, Gramoxone Extra) these two photosynthesis inhibitor herbicides were released by Imperial Chemical Industries of England in nineteen fifty eight. That was the year that I graduated from the University of California at Davis, California and the same year that I joined Chevron Chemical Company. In nineteen fifty nine one of the executives of Imperial Company sent his twenty year old son to my area to learn more about the chemical business in the United States. He stayed at my house and rode with me for two days. He was really startled to see farmers and highway patrol officers with rifles on gun racks in their auto and pick up trucks. In England very few people had access to firearms. He was overwhelmed by our agriculture though. Paraquat became one of our major herbicides, but we didn't call it a photosynthesis inhibitor in those days.

Paraquat and diquat are both named Bipyridyliums. They draw electrons from the photosynthesis chain in the <u>second</u> system which is called Photsystem I. (I don't know who numbered these Photosystem numbers, but everyone has them set up this way.) After leaving the first phase Photosystem II the active chain of molecules in the chloroplast that occupies the leaf cells releases and passes on active electrons to molecules in the chain. The bipyridyliums draw electrons away from the chain and this inhibits the capture and plant use of light energy for the photosynthesis. The positive Paraquat and Diquat then form free radicals with the captured electrons that causes damage to the cell membranes. These photosynthesis inhibitors that cause a final cell membrane damage were originally called (membrane disruptors).

The stable free radical formed by the electron captured by the positively charged bipridinium ion reduces oxygen to a stable free radical that keeps reacting and produces molecules that go on to damage cell membranes of the plant.

Paraquat is used to control all the plants in an area non-selectively. This type of weed control is referred to a “burn down”. Weeds that emerge before the planted crop are targeted by paraquat. It is often the herbicide used in minimum tillage. In noncrop areas both paraquat and diquat can be used as directed sprays. They are also used to repress sods or landscape lawns before reseeding. In the tall casterbean fields we used diquat as a desiccant. Diquat is used in recreation lakes and waterways to control aquatic weeds. Diquat has a lower mammalian toxicity when compared to paraquat. When diluted by water it has a very low toxicity level to mammals and fish.

Application is made directly to the leaves. There is no translocation of either diquat or paraquat. They are both absorbed into the foliage and are not washed off by rain that occurs one hour or even less after application. Grasses are more susceptible to paraquat than the broadleaf weeds or plants.

These two are non selective herbicides and very few plants are tolerant to this herbicide.

Just like Roundup both diquat and paraquat are strong cations and will not leach through the soil. Soil clays with their positive charges hold the negatively charged diquat and paraquat. They are not taken up from the soil by plant life because they are held and become part of the soil. They aren’t even taken up by bacteria in the soil or move in the soil solution. They have a half-life in the soil of three years, but because of their strong tie-up with soil particles planting can occur rapidly.

They are leaf herbicides and the plant leaves will be limp and water soaked after application. Necrosis can be observed within hours of application. They are both fast acting and if drifted to nearby plants necrotic spots will be evident on the plant leaves.

Paraquat is classified by the USA EPA as “restricted use”. It can only be applied by licensed applicators. It is marketed with a blue dye that is added to it in the USA to keep it from being consumed as a beverage like coffee. It has a sharp odor to serve as a warning. It also contains an agent added to it that will cause vomiting if someone drinks it. In most of the countries outside the USA these maerials are not added to paraquat. When I worked for Chevron Spray Company we carried a kit with packets of clay called Fillers Earth and Activated Charcoal to give people who had mistakenly drank fluids with paraquat in them. Paraquat is one of the most used herbicides in use today, because it is an effective weed killer. Only licensed applicators should apply it.

Inhibitors of Protoporphyrinogen Oxidase

The - ase at the end of Oxidase is one way of letting you know that this word is used to describe an enzyme. In this case the enzyme is inside the chloroplast of the plant cell that oxydizes the protoporphyrinogen which produces protoporphrin IX. This very important product is a molecule needed for making chlorophyll (used in photosynthesis) and heme (needed for the electron transfer chain).

This herbicide that inhibits this particular enzyme does more than block the making of chlorophyll and heme. When the enzyme, PPO (protoporphyrinogen oxidase), is inhibited, the protoporphyrin material that the enzyme controls starts growing or accumulating. This material is slowly oxidized by the high concentrations of oxygen (- O2) that are produced in the chloroplast and we now have lots of protoporophrin IX. In the dark without light this increase in this product doesn't do any harm, but light turns it on and the protoporphyrin IX reacts with oxygen two (-O2) turning it into singlet oxygen or (-O1) which is very toxic to plant cells. In this state the oxygen attacks fatty acids and amino acids. The membranes of the plants' cells with unsaturated fatty acids are most vulnerable and we now have a membrane inhibitor. The common name for this herbicide is "Blazer", but it is called a PPO enzyme inhibitor.

Membranes of plant cells

When plants moved from their life in the water to living in the air on land over four hundred million years ago, one of the plant's body needs was the cuticle membrane that keeps water inside its body. Two other evolved body parts included the vascular system that allowed the plants to grow tall because of the transfer of water to the top of the plant by this vascular system with its xylem and phloem, and the other was the ecological development of stomata that are plant controlled openings in the leaf surface called guard cells for the needed exchange of water and oxygen release and the intake of carbon dioxide gas from the air for plant needs.

The cuticle membrane is produced by epidermal cells in plants to coat their body surfaces above the soil level keeping water inside the living plant. Cuticles have three important layers. The outside layer against the air is composed mainly of wax which is an oil material. Inside outer layer is the middle layer containing a mix of both water soluble materials and wax. The third inside layer is made of water soluble materials. The epidermal cells that support the cuticle are located next and they support the cuticle. The cuticle also protects the plant as a physical barrier that resists the invasion of viruses, bacteria and fungi. The cuticle keeps unwanted water, dirt and other microorganisms out of the plant. Roots that are required to take in water do not have cuticle membranes. Roots do have epidermal cells and these cells have cell walls and cell membranes.

All of the plant's cells are contained in the plasma membrane and each individual plant cell has internal membrane system inside the plasma membrane that separate individual parts of the plant cell. These membranes allow water and certain ions and parts of the substrate into the cell and they allow certain substances to be released from the cell. The plasma membrane protects the cell in several ways. They are the connecting agents with the rest of the plant. The membranes keep the contents from spreading throughout the plant causing the death of the plant.

The intercellular membranes include: vacuoles, chloroplasts, mitochondria and the nucleus membranes. The nucleus that contains the genetic information of the cell or the DNA; the RNA information processing needed by the ribosomes to make proteins out of requested amino acids. This membrane has pores in its surface that allows specific DNA information along with the selected ribosome factories to pass out into the cell's cytoplasm to bind amino acids together to form proteins along with the building data.

The vacuoles of the plant are also found in the cell and they have their own membrane. The vacuole take up the largest part of the cell. The vacuole membrane gives support to the plant by its turgor pressure. These vacuoles store ions, sugars, organic and amino acids and a great deal of other products. These products absorb a great deal of water and this causes a large internal pressure build up. As other cells in the plant build up their pressure the total pressure make the cells and entire plant to have rigidity. This gives the plant tissue tension. When plants lose water they will also lose their rigidity from the loss of this pressure in the vacuoles. Vacuole have a special membrane called a tonoplast. Vacuoles can be temporary storage containers or final storage space for plant waste materials. Some herbicides are taken in by plants and stored in cell vacuoles. In storage these herbicides become inactive. Paraquat and diquat weed killers will be stored by some weeds in this way and do not control these weeds because they have this type of vacuole.

A great deal of research is constantly going on in the study of plant cell membranes. How particles are able to penetrate the cell membranes are being researched and new discoveries take place. The building of the more rigid cell walls from material transferred from the surrounding cells through the cell membranes are still being discussed. We do know that material from the living cells are laid out in a long box shape that becomes the home of a growing new cell. The cell wall is made from cellulose and a ground substance and gives the cell and the entire the plant strong support.

The cell membranes primarily contain lipids, but they also contain many proteins.

Cell Membrane Disruptors

These herbicides are also referred to as "burner" type herbicides. The final result of these herbicides is the breakdown of the cell membranes. This causes the death of stems and leaves. They inhibit an enzyme named "protoporphyrinogen oxiddase". They are called "PPOs" . The trade name of some of them include: Goal, Shark and Chateau. They are applied to the growing weed and require good coverage because these chemicals are not easily translocated through the plant. The symptoms of the damage done by these herbicides is the bleaching of the leaves along with desiccation and necrosis where the spray hits the leaves and stems. The damage which includes leaf death should be visible within three to five days.

Both Goal and Chateau can be applied to the soil, but Shark isn't active enough when used as a soil applied herbicide. All three of these herbicides are adsorbed by soil particles and soil organic matter, Goal and Chateau can kill weeds by direct contact with the weed hypocotyl. This is the first part of the weed's leaf to appear just after the germination of the weed seed. If the soil is disturbed after the application of these herbicides the weed control will be reduced.

Of these three herbicides, Goal has the ability to "lift off " the soil after application. This lifting off from the soil after application is called "codistillation". This happens when the molecules of oxyfluorfen in Goal become trapped in water molecules and are carried in these water molecules by evaporation from the soil surface. These water molecules can land on crop foliage or noncrop foliage and result in unwanted damage. This is not the same as spray drift which all applied herbicides are capable of doing. This is another concern when applying Goal as a herbicide.

Root Inhibitor Herbicides

Unlike the top part of the plant the root system is equipped to allow water to enter the plant's system. Roots are also a source of nutrients in the form of minerals while the leafs and stems provide the plant with carbohydrate materials using the process of photosynthesis. The upper part of the plant has a system for keeping water inside the plant once it enters the plant roots. Most of the water taken in by the roots are passed through the plants and released in the stomata outlets in the upper body of the plant in leaves and stems.

When a seed germinates usually the first part of the new plant that emerges from the seed is the radicle followed by the root. In most of the dicot plants one main root is called a taproot. Feeder roots grow from the tap root to increase the surface area of the root system. Tap roots are often modified to be used as a storage part of the plant. The grass monocot plants have a fibrous root system with many smaller roots. The radicle emerges from the seed but doesn't last very long as the tap root or the small adventitious roots take over. Some fibrous roots do become storage vessels. A good example of this is the fibrous rooted sweet potatoe. The new roots can have root hairs that are extensions of the epidermal cells of the roots.

The roots of the growing plant have a tissue at the tip called a root cap. This cap is made up of cells from the meristem cells inside the cap of the root. These meristem cells change first into cells called calumella cells. These calumella cells are then pushed to the tip or periphery of the root cap. Calumella cells are able to detect gravity because they contain amylopasts. They can also respond to light and pressure from soil particles. When these calumella cells are pushed by the growing meristem cells behind them to the periphery of the root cap they become periphery cells and they begin secreting mucigel. Mucigel prevents desiccation or drying out. In some varieties of plant the mucigel has a material that can prevent the growth of other plant roots that compete for growing space. Mucigel lubricates the root. Then the new roots can penetrate the soil improving root growth and this increases the absorption or water and nutrients. Helping in the dissolving of ions by the chelation that mucigel is able to carry out aids in uptake by the plant's needed water and nutrients. Mucigel has nutrients in it that can be used by soil mycorrhizae and symbiotic bacteria that aid the growing plant.

There is an area just behind the root cap named the quiescent center that is an area of inactive cells. These cells become replacements for the meristem cells of the roots. Three other regions behind these quiescent cells are zones of cell division. These cells are derived from the root apical meristems that grow downward. Apical meristem cells are also located at the top of the plant that provides upward growth. As these cells elongate they shove the root cap into the soil. This area behind the root cap is where root hairs that increase the ability of the plant to increase water and nutrient uptake multiply. This also becomes the first area for the xylem tissue to form and start moving water to the top growth of the plant.

The plant depends on water as its major item of survival. When the plant evolved into a living organ that could exist and multiply in air and on land it developed a body that was able to obtain the water it required and the root became it's main tool in gaining that water. The three primary tissues of the root come from the root apical meristem cell system immediately behind and in the area where cells mature in the root tip. The three systems are the protoderm, the ground meristm and the procambion.

The root like the rest of the plant has an epidermis which is made from the protoderm. The epidermis cover the young cell and is one cell thick. The epidermis has growths called root hairs. These hairs are extensions of the epidermis cells that increase the surface of the epidermis cells by growing out into the surrounding soil. This increase in the plants root surface allows more water and soil nutrients to enter the plant. The root's epidermal cells are there to allow water and nutrients to enter the living plant.

Inside of the epidermis of the root is the cortex. The cortex is located just inside epidermis. It is formed from the ground meristem cells and has three layers called the (1) hyperdermis, (2) the storage parenchyma cells and the (endodermis). The hypodermis is a layer of cells containing suberin that helps keep water inside the cortex. The storage parenchyma cells are thin walled and store starch. The endodermis is the layer of cells that is the innermost part of the cortex.

The endodermis is made up of a single cell sheet that is closely packed together without any air space between them. Plant cell walls are water soluble but the endodermis cell walls on all four sides where the square shaped cells come together are sealed with suberin and lignin material forming a water proof seal called the caspariun strip. This endodermis barrier required that any liquid or solid most go into the outside surface of the cell and out through the back of the cell. Nothing can go through the space between the cell's ends because of the casparion strip. Everything must go through the endodermis cell's outer and inner membrane and its cytoplasm in order to enter the plant root's xylem tissue. This allows the root to use the endodermis cell membrane to control absorption of liquid materials and solid materials for the living plant. The endodermis membrane and the living cell organs and cytoplasm of the endodermis cell can control what enters the total plant from the soil. The soil water and its contents have to go through the outer endodermis cell membrane to enter the endodermis cell and another inner endodermis cell membrane to enter the plant's internal system.

In the root of the plant all tissues inside the endodermis make up an area called the <u>stele</u>. These tissues that are inside the stele include the pericycle and the plant vascular system. The pericycle located just inside the endodermis has a layer of meristem cells that when triggered develop into lateral roots. Lateral roots are not root hairs. DNA and environmental conditions trigger the growth of lateral roots. Once these lateral roots start to grow they break through the endodermis and the cortex to the epidermis and start a new root that has its own epidermis, cortex, endodermis and root hairs. These lateral roots will grow out as they extend into the soil. In the event that the original tap root is injured the lateral roots will take over the duties of the original root.

The vascular system that is inside the root pericycle is make up of the xylem that is used by the plant to transport water up from the roots throughout the plant and the phloem that transports food throughout the plant. In the dicot or broadleaf plants a cross section view will show the xylem is in the center of the root and is star shaped with the phloem surrounding the star and in between the rays of the xylem star. This is a bottom to top view.

The monocot, narrow leaf plants do not have a set order for the placement of phloem and xylem. The phloem vascular tube may be in any location of the system and the xylem can be in the inside or the outside of the system. The plant and its parts depending on whether it is a broad leaf plant like cotton or a narrow leaf plant like wheat has a vascular system inside each part to provide a transfer system moving needed items around inside of the plant.

Plant mitosis and meiosis

The growth of a plant whether it is the root, fruit, stem, leaf or vascular system is done by adding cells to these plant parts. The growth of the plant parts is done by doubling the plant cells in these plant parts. A particular cell goes through the process of doubling itself this procedure is called mitosis. One particular cell becomes two of that particular cell with the same number of chromosomes.

Chromosomes are made up of DNA and proteins. They are the plants source of genetic information. Each new cell contains the same genes that control the production of a specific type of plant product or animal product. Whatever the plant needs is developed under the direction of the chromosome.

Some of the plant cells never divide or go through mitosis, but they still may increase in size. Plants and animals also have sexually producing organisms called gametes (sperm or eggs) and these cells divide by a process called meiosis, but in the meiosis process four cells are produced instead of two cells. For this discussion of weed herbicides we will only discuss the mitosis process of plant growth.

Plant cells have life cycles just like the other cell organisms. They live most of their time in an interphase which is divided into three stages. The first stage is called the first gap or gap one; the second is the synthesis; and the third is named gap two. During the first stage or gap one the plant cell goes through its normal duties or functions that keeps it alive and it may gain in size. During the second life stage of synthesis the DNA replicates itself. Now we have double the amount of chromosomes joined together at their midpoints with a fastener called a kinetochre. In the last stage, gap two, The cell makes the items necessary to carry out the mitosis. These include the spindle fibers and two poles.

In the prophase the nuclear membrane disappears. In the prometaphase the spindle is set up in the region where the nuclear membrane was. The poles are now are at either end of the old nuclear membrane area. The pairs of chromosomes are joined together in their middles facing opposite poles. The spindle fibers are attached to the poles and the kinetochores on the chromosomes.

In the metaphase chromosomes line up in the middle and the spindle fibers start shrinking. A plate forms in the middle called the metaphase plate.

The chromosomes part as the plate divides the chromosomes during the anaphase.

The spindle fibers shrink pulling the split chromosomes to either pole in the telephase. The spindle fibers and poles fall apart and two new nuclear membranes form around the chromosomes and two cells are formed with a new plant cell membrane around both new cells. The chromosomes begin giving messages building two new cells which include the nucleous with its two chromosomes and protein building ribosomes. The surrounding cytoplasm will contain proteins, amino acids. Vacuole, a new wall around each cell and the other organs of a plant cell will form as two cells and mitosis will have taken place.

Root herbicides are able to inhibit the mitosis action of the plant cell. These root mitosis inhibitors are named dintroanalines. They do this by inhibiting the formation of the **spindle fibers**. These fibers are made from tubulin. By stopping the production of tubulin the cell ends up with root cells with double chromosomes and faulty cell walls that can't continue to grow or absorb nutrient. This results in plant root tips that are clubbed and swollen and the common visual signs of nutrient deficiencies. These include: yellow or purple leaves, whitening due to loss of chlorophyll and weak stems due to poor cell walls.

There are several herbicides in the dinitroaniline group. Trade names include: Balan, Treflan, Prowl and Surflan. Balan is a lettuce approved herbicide and it works by inhibiting the tubulin spindle fibers that are necessary for the completion of cell mitosis. Balin is taken up by the plant's roots, but it is not transported throughout the plant and therefore does it's inhibiting in the roots. The signs of this damage include the clubbed, swollen appearance of the roots. When the weed first emerges from its seed the stem area just below the seed or cotyledon leaves will show some swelling. The stem just above ground can be stunted and show brittleness. The Balan damage to the treated plant's stems will show more damage than treatment with Prefar or Kerb. Balan is strongly held by the soil particles and once it has a location in the soil it will not move with the soil water.

Kerb is a substituted amide and not a dinitroaniline like Balan, but it also is a plant root inhibitor that will inhibit the mitosis of the plant cells. Kerb is water soluble and will move in the soil with the water. It is applied to the soil surface in the sprinkler irrigation system. Too much water from the sprinklers will put the Kerb below the weed seeds and result in poor herbicide control.

Prefar is a substituted amide that will inhibit the mitosis process of root growth. When applied to the soil it does not move up into the plant. Prefar will kill lateral roots, but the tap root is strong enough to grow through an application of Prefar. It is absorbed by roots only and it stops cell division, but the exact process isn't known. All three of these herbicide dinitroanilines (Balan, Treflan, Prowl) substituted amides (Kerb and Prefar) can cause crop injury. Poor growing conditions or applying more than the label recommends will result in a damaged crop, but when used properly these herbicides are excellent weed control tools.

Amino Acid Synthesis Inhibitors.

These herbicides control weeds by blocking the production of vital enzymes needed by plants to produce needed amino acids. Plants and animals need twenty different amino acids. Plants because they take in nitrogen can make all twenty in their systems. Animals can make twelve of these vital amino acids. Animals get the other eight from eating plants or other animals that have eaten plants.

The amino acids that these herbicides inhibit are not produced in animals therefore the enzymes needed to produce these amino acids do not exist in animals and this is one of the safety qualities of these herbicides. When a plant cell produces a protein it uses its ribosomes to put together amino acids using instructions from the plant DNA. The amino acids are built in separate processes. Some of this amino acid construction can require several processes before the full completion of the structure of the amino acid. Enzymes are needed to complete each of these activities. Only one particular enzyme is needed for each phase of the development and when any of these enzymes is tampered with the whole process is destroyed.

Round Up binds with one of the enzymes needed in the construction of one of the seven phases in the pathways to the manufacture of amino acids in growing plants. This binding occurs in the last phase of the seven phases of construction. This enzyme tie-up destroys the total construction of the seven pathways. In this case more than a loss of thirty five percent of the dry weight of the entire plant is destroyed causing the death of the target weed. Three essential amino acids- phenylalanine, tyrosine and tryptophan- plus many secondary metabalates in the plant are lost due to this tie-up of the enzyme named "EPSPS",

All of the amino acids are constructed in phases some only have a few phases in their pathways of construction and others have several phases of construction. The damage to the plant takes place in a week to two weeks.

The other amino acid synthesis inhibitors are called ALSs. They act on a specific enzyme acetolactate synthase (ALS) that is needed by the plant to produce three amino acids that are named: valine, leucine, and isoleucine. The damage to the plant caused by these herbicides include effects to seedling growth, plant stunting and reduced seed production. They can travel in the plant xylem or phloem whereas Round Up travels in the phloem. The major drawback to these herbicides is that they are so specific on what they will inhibit that the weeds become resistant to them by growing weeds that do not need this particular enzyme. Different weeds can exist with the use of different enzymes. Round Up resistance is caused by the same problem.

The brand names of these ALSs include: (Sulfonylureas); Glean, Finesse, Ally, Amber, Harmony, Extra, Express, Peak and (Imidazolinones)

Assert.

Your hour is completed.

The use of trade names in this course is solely for the purpose of providing specific information. It is not a guarantee or warranty of the products named, and does not signify that they are approved to the exclusion of others of suitable composition. Use pesticides safely. Read and follow directions on the manufacturer's label.

References:

http://en.wikipedia.org/wiki/auxin

http://en.wikipedia.org/wiki/Herbicide#

http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3146736/

http://ag.arizona.edu/crop/vegetables/weeds/lettuceinjury.html

http://www.imbio.uni-bonn.de/molekulare-biotechnologie/forschung/plant-lipids

http://www.sbreb.org/brochures/herbicide/lipid.htm

http://www.extension.umn.edu/distribution/cropsystems/components/696701j.html

http://agron-www.agron.iastate.edu/Courses/agron317/Lipid Inhibitors.htm

http://www2.lsuagcenter.com/subjects/weedscience/pdf/AGRO4070/Handout18.pdf

http://www.btny.purdue.edu/weedscience/moa/Photosynthetic Inhibitors/text.html

http://www.btny.purdue.edu/weedscience/moa/Photosynthetic Inhibitors/text.html

http://agron-www.agron.iastate.edu/Courses/Agron317/Photosynthesis_Inhibitors.htm

http://passel.unl.edu/pages/informationmodule.php?idinformationmodule=939154153&topicorder=5&maxto=8

http://en.wikipedia.org/wiki/Photosynthetic_reaction_center

http://passel.unl.edu/pages/informationmodule.php?idinformationmodule=939154153&topicorder=3&maxto=8

http://www.cwss.org/proceedingsfiles/2006/64_2006.pdf

http://hortweeds.tennessee.edu/webapp/test/moa.htm

http://ohioline.osu.edu/weeds/weeds_13.html http://en.wikipedia.org/wiki/Pendimethalin

http://www.cwss.org/proceedingsfiles/2006/64_2006.pdf

https://www.pioneer.com/CMRoot/Pioneer/US/products/stewardship/Oklahoma_Herbicide_MOA.pdf

http://www.hindawi.com/journals/ija/2012/305764/

https://www.pioneer.com/CMRoot/Pioneer/US/products/stewardship/Oklahoma_Herbicide_MOA.pdf

http://faculty.clintoncc.suny.edu/faculty/michael.gregory/files/bio%20102/bio%20102%20lectures/plant%20structure/plant%20structure.htm

http://facweb.furman.edu/~lthompson/bgy34/plantanatomy/plant_root.htm

http://www.btny.purdue.edu/weedscience/moa/Root_Mitotic_Inhibitors/text.html

http://www.biologie.uni-hamburg.de/b-online/e23/23.htm

http://en.wikipedia.org/wiki/Plant_cuticle

http://www.cmg.colostate.edu/gardennotes/132.html

https://www.extension.purdue.edu/extmedia/WS/WS-23-W.html

http://www.planta.cn/forum/files_planta/7_502.pdf

http://passel.unl.edu/pages/informationmodule.php?idinformationmodule=1030652583&topicorder=3&maxto=5

http://pubs.cas.psu.edu/freepubs/pdfs/uc175.pdf

http://lifeofplant.blogspot.com/2011/03/mitosis-and-meiosis.html

http://www.extension.umn.edu/distribution/cropsystems/components/6967_01g.html

Gardner, Franklin P, Pearce, R. Brent, Mitchell, Roger L. *Physiology of Crop Plants,*

IOWA STATE UNIVERSITY PRESS: AMES 1985

http:en.wikipedia.org/wiki/Plant_cuticle