# Basic summary of Plant Defenses: methods used by plant against Pathogens and Herbivores

**[a]Jayesh Kumar, [b]Ajay Kr Srivastava, [c]Shila Kumari**
[a]Department of Life Science ,Central University of Jharkhand, Ranchi- 835222 , Jharkhand , India
[b]Head, PG Department of Botany, St. Xaviers College.Ranchi, Jharkhand, India
[c]Department of Botany , Doranda College Ranchi,Jharkhand, India
**Corresponding Author :** Jayesh Kumar

## Abstract

Directly or indirectly, plants provide comprehensive source of food, nutrients and non-food product such as textiles, medicines, rubber, soaps, inks, dyes, chemicals and wood to the entire organism. Since plants are a rich source of nutrients to most organisms, it remains a prime target for herbivores and infectious Pathogenic agents. Though lacking a proper immune system, plants have developed an array of constitutive and inducible defenses to fend off such attacks. Plants respond to extraneous invasions through various morphological, biochemical and molecular mechanisms to counter the effects of pathogens and herbivores attack. Basic know-how of the mechanisms that plant employs to defend themselves from pathogens and herbivores are paramount to protect food supply and development of highly disease-resistant plant species.

**KEYWORDS:** Pathogen, Herbivores, Disease, Immunity, Constitutive and Inducible defense

## Introduction

Plants are the rich warehouse of nutrients for many organisms including bacteria, fungi, protists, insects, and vertebrates. Though plants lack an immune system in comparison to animals, they have developed a wide array of structural, chemical, and protein-based defense mechanisms designed to detect invading organisms and prevent them before they cause extensive damage. Humans, almost exclusively, depend on plants for food and nutrition. Nonetheless, plants provide many important non-food products including textiles, medicines, industrial chemicals, cosmetics, soaps, rubber, plastics, inks, dyes and wood. Imperative to the understanding about the methods plants adopt to defend themselves from pathogens and herbivores is essential in order to protect our food supply and develop highly disease-resistant plant species.

The present article introduces the concept of plant disease and scrutinizes some of defense mechanisms common among higher plants. A close examination to plant anatomy is reviewed, as well as some of the ecological relationships that imparts to plant defense and disease resistance. Special emphasis has been laid to illustrate how products derived from substances produced by plants during defense responses are used in everyday life.

## Plant Disease vs. Defenses and types

In broad terms, **disease** refers to any physiological abnormality or significant disruption in the "normal" health of a plant. The causative agent of disease may be by living (**biotic**) agents, including fungi and bacteria, or by environmental (**abiotic**) factors such as nutrient deficiency, and stresses such as drought, lack of oxygen, excessive temperature, ultraviolet radiation, or pollution. In order to protect and minimize themselves from damage, plants have developed a wide array of constitutive and inducible defenses. **Constitutive** defenses comprises of many preformed barriers such as cell walls, waxy epidermal cuticles, and bark. These substances are not required only to protect the plant from invasion but they also give the plant strength and rigidity. Additional to the abovementioned preformed barriers, virtually all living plant cells have the ability to detect invading pathogens and respond with **inducible** defenses including the production of toxic chemicals, pathogen-degrading enzymes, and deliberate cell suicide. Plants often wait till pathogens are detected before producing toxic chemicals or defense-related proteins due to the high energy costs and nutrient requirements associated with their production and maintenance.

**Pathogens attack versus Plant mechanism**

Many plant pathogens work "silently" with specialized tools designed to disable the plant's security system and unlock the vault without being detected. Similarly, many pathogens establish intimate connections with their hosts in order to suppress plant defenses and promote the release of nutrients. Pathogens that keep their host alive as well as feed on living plant tissue are called **biotrophs**. Examples of biotrophic pathogens include the powdery mildew fungus *Blumeria graminis* and the bacterial rice pathogen *Xanthomonas oryzae*. Other pathogens resort to brute force, often producing toxins or tissue-degrading enzymes that overwhelm plant defenses causing the quick release of nutrients. These pathogens are called **necrotrophs**, and examples include the gray mold fungus *Botrytis cinerea* and the bacterial soft-rot pathogen *Erwinia carotovora*. Some pathogens are biotrophic during the early stages of infection but become necrotrophic during the latter stages of disease. These pathogens are called **hemibiotrophs** and include the fungus *Magnaporthe grisea*, the causative agent of rice blast disease.

Figure 1. Powdery mildew on a maple leaf

Figure 2. Rice blast disease on rice leaves

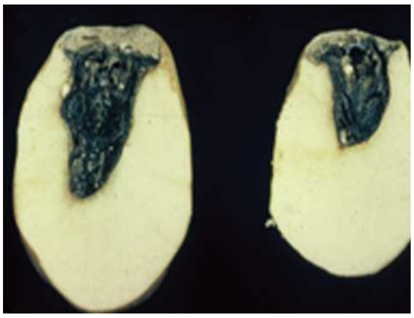

Figure 3. Blackleg soft-rot on a potato tuber

Most biotrophic and hemibiotrophic pathogens infect and causes disease on a relatively small group of host plants because of the slightly different set of specialized genes and molecular mechanisms required for each host-pathogen interaction. The

**host range** refers to the plant species on which a pathogen is capable of causing disease. For example, brome mosaic virus (BMV) infects grasses such as barley but not legumes. A plant species that does not show disease when infected with a pathogen is referred to as a **non-host plant** species for that pathogen. Organisms that do not cause disease on any plant species, such as the saprophytic bacterial species *Pseudomonas putida*, are referred to as **non-pathogens**.

When a pathogen invades to cause disease on a particular host species, two outcomes are possible: A compatible response is an interaction that results in disease, while an incompatible response is an interaction that results in little or no disease at all. Although a particular plant species may be a susceptible host for a particular pathogen, some individuals may harbour genes that help recognize the presence of the pathogen and activate defenses. For example, some tomato cultivars show disease when infected with the bacterial pathogen.

Pseudomonas syringae (a compatible response), but others (such as cultivar Rio Grande) are capable to recognize the bacteria and limiting disease via resistance (an incompatible response). Disease resistance are a continued process of responses ranging from immunity (the complete lack of any disease symptoms) to highly resistant (some disease symptoms) to highly susceptible (significant disease symptoms).


Figure 4. Tomato leaves exposed to the bacterial pathogen P. syringae. The leaf on the left is diseased, and the leaf on the right is resistant.

Plants have an organised multiple layers of sophisticated surveillance mechanisms that recognize potentially dangerous pathogens and rapidly respond before those organisms get a chance to cause serious damage. These surveillance systems are linked to specific pre-programmed defense responses. **Basal resistance**, also known as **innate immunity**, is the first line of pre-formed and inducible defenses that protect plants against entire groups of pathogens. Basal resistance is triggered when plant cells encounters and recognize **microbe-associated molecular patterns (MAMPs)** including specific proteins, lipopolysaccharides, and cell wall components commonly found in microbes. As a result , the living plant cells become fortified against attack. Pathogens as well non-pathogens are capable of triggering basal resistance in plants due to the widespread presence of these molecular components present in their cells.

Figure 5. Bacterial flagella are often recognized by plants during basal resistance.

Interestingly, some countermeasures have been developed by pathogens that are able to suppress basal resistance in certain plant species. If any of the pathogen is capable of suppressing basal defense, plants may respond with another line of defense: the hypersensitive response (HR). The hypersensitive response is characterized by deliberate plant cell suicide at the site of infection. Although drastic compared to basal resistance, the HR may limit pathogen access to water and nutrients by sacrificing a few cells in order to save the rest of the plant. The HR is typically more pathogen-specific than basal resistance and is often triggered when gene products in the plant cell recognize the presence of specific disease-causing effector molecules introduced into the host by the pathogen. The pathogens capable of inducing the HR in plants include Bacteria, fungi, viruses, and microscopic worms called nematodes.

Once the hypersensitive response has been triggered, plant tissues may become highly resistant to a broad range of pathogens for an extended period of time. This phenomenon is called **systemic acquired resistance (SAR)** which represents a heightened state of readiness where plant resources are mobilized in case of further attack. Researchers have learned to artificially trigger SAR by spraying plants with chemicals called **plant activators**. These substances are gaining favor in the agricultural community because they are much less toxic to humans and wildlife than fungicides or antibiotics, and their protective effects can last much longer.

Apart from the hypersensitive response, **RNA silencing** is a sophisticated genetic defense mechanisms from which plants can defend themselves against viruses. Many of the viruses produce double-stranded RNA or DNA during replication in a host cell. Plants recognizes these foreign molecules and respond by digesting the genetic strands into useless fragments , thereby halting the infection. Plants that are infected with viruses often exhibit chlorosis and mottling, but disease symptoms may eventually disappear if RNA silencing is successful, a process called **recovery**. In addition, the plant may retain a template of the digested genetic strand that can be used to quickly respond to future attack by similar viruses, a process analogous to the memory of vertebrate immune systems.

**Detection of Insect Herbivores**

Mechanical damage caused by insects are not usually considered “true” plant disease, although plants have developed surveillance systems designed to recognize insect pests and respond with specific defense mechanisms. Plants are able to distinguish between general wounding and insect feeding by the presence of **elicitors** contained in the saliva of chewing insects. In response, plants may release **volatile organic compounds (VOCs)**, including monoterpenoids, sesquiterpenoids, and homoterpenoids. These chemicals may repel harmful insects or attract beneficial predators those which may prey on the destructive pests. For example, wheat seedlings infested with aphids may produce VOCs that repel other aphids. Lima beans and apple trees emit chemicals that attract predatory mites when damaged by spider mites, and cotton plants produce volatiles that attract predatory wasps when damaged by moth larvae. Feeding on one part of the plant can induce systemic production of these chemicals in other undamaged plant tissues, and once released, these chemicals can act as signals to neighbouring plants to initiate producing similar compounds. Production of these chemicals requires a high metabolic cost to the host plant, so many of these compounds are not produced in large quantities until after the insects have begun to feed.

**Structural Defenses**

**The Plant Cell**

All plant tissues consist pre-formed structural barriers that limits or reduce pathogen attachment, invasion and infection. The **cell wall** constitutes major line of defense against fungal and bacterial pathogens. It is an excellent structural barrier that also incorporates a wide variety of chemical defenses that can be rapidly activated when the cell detects the presence of potential pathogens. All plant cells have a **primary cell wall**, which provides structural support, essential for turgor pressure, and many also form a **secondary cell wall** that develops inside of the primary cell wall after the cell stops growing. The primary cell wall consists mostly of **cellulose**, a complex polysaccharide consisting of thousands of glucose monomers linked together to form long polymer chains. These chains are bundled into fibers called **microfibrils**, which give strength and flexibility to the wall. The cell wall may also contain two groups of branched polysaccharides: cross-linking glycans and pectins. **Cross-linking glycans** include **hemicellulose** fibers that give the wall strength via cross-linkages with cellulose. **Pectins** forms hydrated gels that help "cement" neighbouring cells together and regulate the water content of the wall. Soft-rot pathogens often target pectins for digestion using specialized enzymes that cause cells to break apart: these organisms are extremely common, and anyone who has seen fruits or vegetables become brown have seen these pathogens in action.

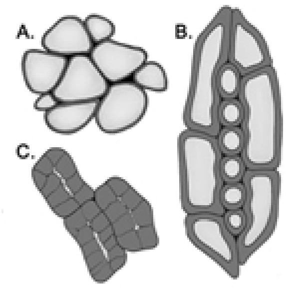


Figure 6. Comparison of cell wall types. The primary cell walls of red pepper cells (A) are relatively thin compared to the thick secondary cell walls of oak wood (B). The walls of pear fruit stone cells (C) are so thick that the cell lumen is barely visible.

Plant cell walls usually also contain **lignin**, a heterogeneous polymer composed of phenolic compounds that gives the cell rigidity. Lignin is the primary component of wood, and cell walls that become "lignified" are highly impermeable to pathogens and difficult for small insects to chew. **Cutin, suberin**, and **waxes** are fatty substances that may be deposited in either primary or secondary cell walls (or both) and outer protective tissues of the plant body, including **bark**.

Cell walls contain proteins and enzymes that intensively work to reshape the wall during cell growth yet thicken and strengthen the wall during induced defense. When a plant cell detects the presence of any potential pathogen, enzymes catalyze an **oxidative burst** that produces highly reactive oxygen molecules , capable of damaging the cells of invading organisms. Reactive oxygen molecules also help strengthen the cell wall by catalyzing cross-linkages between cell wall polymers, and they serve as a signal to neighboring cells that an attack is underway. Plant cells also respond to microbial attack by rapidly synthesizing and depositing **callose** between the cell wall and cell membrane adjacent to the invading pathogen. Callose deposits, called **papillae**, are polysaccharide polymers that impede cellular penetration at the site of infection, and these are often produced as part of the induced basal defense response.

Some plant also contains cells highly specialized for plant defense. **Idioblasts** ("crazy cells") help protect plants against herbivory because they contain toxic chemicals or sharp crystals that tear the mouthparts of insects and mammals as they feed. Many classes of idioblasts includes pigmented cells, sclereids, crystalliferous cells, and silica cells. **Pigmented cells** often contain bitter-tasting tannins that make plant parts undesirable as a food source. Young red wines often contain high levels of tannins that give wine a sharp, biting taste. **Sclereids** are irregularly-shaped cells with thick secondary walls that are difficult to chew: the rough texture of pear fruit (*Pyrus* spp.) is caused by thousands of sclereid **stone cells** that can abrasively wear down the teeth of feeding animals. Stinging nettles (*Urtica dioica*) produce **stinging cells** shaped like hypodermic needles that break off when disturbed and inject highly irritating toxins into herbivore tissues. Some stinging cells contain **prostaglandins**, hormones which amplify pain receptors in vertebrate animals causing the increase sensation of pain. **Crystalliferous cells** contain crystals of calcium oxalate that may tear herbivore mouthparts when chewed and can be toxic if ingested. Members of the genera *Philodendron* and *Dieffenbachia* are very common tropical house plants that contain large amounts of these cells. Humans and pets who chew the leaves of these plants may experience a burning sensation in the mouth and throat that is often accompanied by swelling, choking, and an inability to speak. For these reasons, species of Dieffenbachia are commonly called **dumb cane**. Grasses and sedges contain rows of **silica cells** in their epidermal layers, giving strength and rigidity to the growing leaf blades and deter feeding by chewing insects.

**Plant Tissues and Specialized Appendages**

**The epidermis** constitutes the outermost protective tissue system of leaves, floral parts, fruits, seeds, stems, and roots of plants until they undergo considerable secondary growth. It is also considered first line of defense against invading pathogens and consists of both specialized and unspecialized cells. The epidermal cells of aerial plant parts are often covered in a waxy cuticle that not only ceases water loss from the plant, but also prevents microbial pathogens from coming into direct contact with epidermal cells and thereby limits infection. The cuticle can be relatively thin (aquatic plants) or extremely thick (cacti). The hydrophobic nature of the cuticle also prevents water from collecting on the leaf surface, an important defense against many fungal pathogens that require standing water on the leaf surface for spore germination. However, some fungal pathogens including *Fusarium solani* produce cutinases that degrade the cuticle and allow the fungi to penetrate the epidermis.

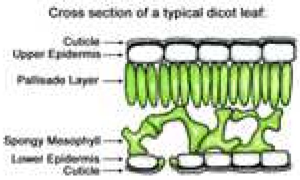


Figure 7. The epidermis is a protective layer of cells that is usually covered with a thin, water-resistant cuticle that helps prevent water loss from the plant.

Interspersed among the many unspecialized cells of the epidermis are **guard cells** which regulate gas exchange through small openings called **stomata**. These pores allow carbon dioxide to enter the leaf for use in photosynthesis while restricting excessive water loss from the plant. Stomatal pore size is highly regulated by plants, and guard cells can participate in defense by closing in response to the presence of MAMPs.

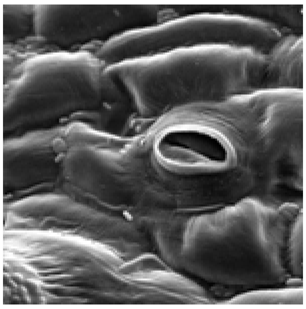

Figure 8. Stomata on the surface of a tomato leaf. Note the small rod-shaped bacteria.

**Trichomes** ("leaf hairs") are specialized epidermal cells found on aerial plant parts that may provide both physical and chemical protection against insect pests. The velvety appearance of dusty miller (*Senecio cineraria*) is caused by thousands of tiny trichomes covering the plant's surface. Trichomes on the surface of soybeans (*Glycine max*) prevent insect eggs from reaching the epidermis and the larvae starve after hatching. The hook-shape of snap bean (*Phaseolis vulgaris*) trichomes impale caterpillars as they move across the leaf surface, and **glandular trichomes** in potato and tomato secrete oils that repel aphids. In woody plants, the **periderm** replaces the epidermis on stems and roots. Outer bark (**phellem**) is an excellent example of a preformed structural barrier that contains high amounts of water-resistant **suberin** and prevents many pathogens and insects from reaching the living cells underneath.

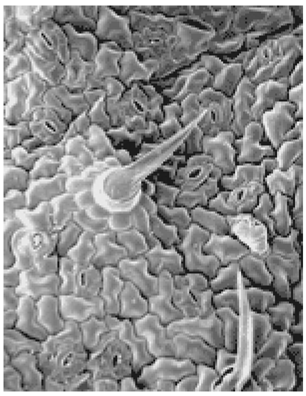

Figure 9. *Phaseolis vulgaris* bean leaf surface with stomata and uniseriate trichomes.

**Thorns** are modified branches that protect plants from grazing vertebrates. Many cacti produce thorn-like structures that are actually modified leaves or parts of leaves (e.g., stipules) called **spines** which serve similar purposes, such as in the barrel cactus (*Ferocactus* spp.). Botanically, the “thorns” on the stem of rose plants (*Rosa* spp.) are neither true thorns nor spines: they are basically outgrowths of the epidermis called **prickles**.

**Chemical Defenses**

Plant chemicals may be broadly categorised into two groups: primary metabolites and secondary metabolites. Substances produced by all plant cells that are directly involved in growth, development, or reproduction are **Primary metabolites**. Examples include sugars, amino acids , proteins  and nucleic acids. **Secondary metabolites** are often involved with plant defense and are not directly involved in growth or reproduction. These compounds usually belong either of the  three large chemical classes: **terpenoids, phenolics, and alkaloids.**

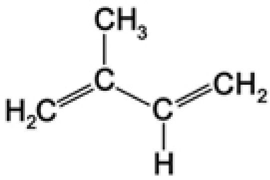


Figure 10. Isoprene

**Terpenoids (terpenes)** represent the largest class of secondary metabolites with over 22,000 described compounds and occur in all plants. The simplest of it  is the hydrocarbon **isoprene** ($C_5H_8$), a volatile gas emitted during photosynthesis in large quantities by leaves that may protect cell membranes from damage caused by high temperature or light. Terpenoids are classified by the number of isoprene units that construct them. For example, **monoterpenoids** consist of two isoprene units, **sesquiterpenoids** (three units), **diterpenoids** (four units), and **triterpenoids** (six units).

Monoterpenoids and sesquiterpenoids are the primary components of essential oils, which are highly volatile compounds that imparts  the fragrance to plants that produce them. Essential oils usually function as insect toxins and many protect the plant against fungal or bacterial attack. Mint plants (Mentha spp.) produce large quantities of the monoterpenoids menthol and menthone which are produced and stored in glandular trichomes on the epidermis. Pyrethrins are monoterpenoid esters produced by chrysanthemum plants that act as insect neurotoxins. Many commercially available insecticides are infact synthetic analogues of pyrethrins, called pyrethroids, including the insecticides permethrin and cypermethrin. Pine tree resin contains large quantities of the monoterpenoids alpha- and beta-pinene, which are potent insect repellents; these compounds give the organic solvent turpentine its characteristic odour.

Apart from usage of Monoterpenoids as insecticides, many seasonings, spices,condiments and perfumes are made using essential oils that function as insect toxins in plants but are relatively harmless to humans. Examples include basil (*Ocimum* spp.), peppermint and spearmint (*Mentha* spp.), rosemary (*Rosmarinus* spp.), oregano (*Origanum* spp.), sage (*Salvia* spp.), savory (*Satureja* spp.), thyme (*Thymus* spp.), black pepper (*Piper* spp.), cinnamon (*Cinnamomum* spp.), and bay leaf (*Laurus* spp.).

**Diterpenoids** include **gossypol**, a terpenoid produced by cotton (*Gossypium hirsutum*) that has strong antifungal and antibacterial properties. **Triterpenoids** are similar in molecular structure to plant and animal sterols and steroid hormones. **Phytoectysones** are mimics of insect molting hormones which when produced by plants such as spinach (*Spinacia oleracea*), they disrupt larval development and increase insect mortality. The fresh scent of lemon and orange peels is the result of a class of triterpenoids called **limonoids. Azadirachtin** is a very powerful limonoid isolated from neem trees (*Azadirachta indica*): some insects are repelled by concentrations as low as a few parts per million. **Citronella** is an essential oil isolated from lemon grass (*Cymbopogon citratus*); it contains high limonoid levels and has become a popular insect repellent due to its low toxicity in humans and biodegradable properties.

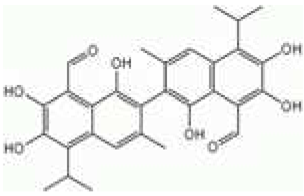

Figure 11. Gossypol

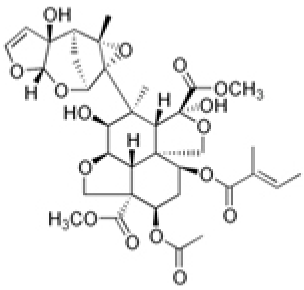

Figure 12. Azadirachtin

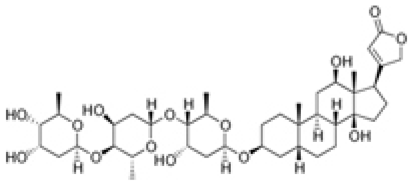

Figure 13. Digoxin

Insects are not the exclusive herbivores that feed onto plants. Triterpenoids such as cardiac glycosides are highly toxic to vertebrate herbivores, including humans, and can cause heart attacks if ingested in high quantities. Foxglove (Digitalis purpurea) is the principal source of the cardiac glycosides **digitoxin** and **digoxin**, which are used in small quantities to treat heart disease in people medicinally.

Saponins are glycosylated triterpenoids present in the cell membranes of many plant species. These substances have detergent (soap-like) properties that disrupt the cell membranes of invading fungal pathogens. The wheat pathogen *Gaeumannomyces graminis* is unable to infect oats that contain avenacins, a class of triterpenoid saponins. However, some fungal pathogens have developed counter measures to these plant defenses , eg., Botrytis cinerea, Fusarium oxysporum, and *Septoria lycopersici* are all capable of degrading saponins and causing disease in susceptible saponin-producing plants.

**Phenolics** , another large class of secondary metabolites which are produced by plants to defend themselves against pathogens. They are produced via the shikimic acid and malonic acid pathways in plants, and include a wide variety of defense-related compounds including flavonoids, anthocyanins, phytoalexins, tannins, lignin, and furanocoumarins. **Flavonoids** are one of the largest classes of phenolics. **Anthocyanins** are colourful water-soluble flavonoids pigments produced by plants to protect foliage from the damaging effects of ultraviolet radiation. Anthocyanins are responsible for the attractive colours of many plants and are present in high concentrations in flowers, fruits, and the leaves of deciduous plants. **Phytoalexins** are **isoflavonoids** with antibiotic and antifungal properties are produced in response to pathogen attack. These toxic molecules disrupt pathogen metabolism or cellular structure but are often pathogen specific in their toxicity. Examples include **medicarpin** produced by alfalfa (*Medicago sativa*), **rishitin** produced by both tomatoes and potatoes (the *Solanaceae* family), and **camalexin**, produced by *Arabidopsis thaliana*.

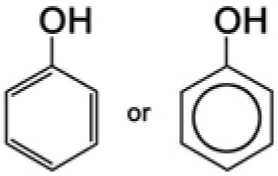


Figure 14. Phenol, the simplest phenolic compound

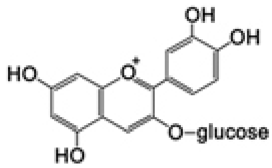


Figure 15. Cyanin glycoside, an anthocyanin

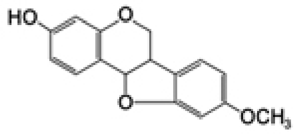


Figure 16. Medicarpin, a phytoalexin

Plants producing **Tannins** are water-soluble flavonoid polymers which are stored in vacuoles. Tannins are toxic to insects because they bind to salivary proteins and digestive enzymes including trypsin and chymotrypsin resulting inactivation of protein. Insect herbivores that ingest high amounts of tannins fail to gain weight and eventually die. The sharp taste of red wine is caused by grape tannins binding to salivary proteins in the mouth resulting in protein coagulation.

**Lignin**, a highly branched heterogeneous polymer found mainly in the secondary cell walls of plants, although sometimes primary walls can also become lignified. It consists of hundreds or thousands of phenolic monomers and is a primary component of wood. Due to its insolubility, rigidity, and virtual indigestibility, lignin acts as an excellent physical barrier against pathogen attack.

**Furanocoumarins** are phenolic compounds produced by a large swathe of plants in response to pathogen and herbivore attack. Activated by ultraviolet light ,they can be highly toxic to certain vertebrate and invertebrate herbivores due to their integration into DNA, which contributes to rapid cell death. In fact, grapefruit juice contains small quantities of furanocoumarins, greatly increase the absorption of certain drugs into the bloodstream from the intestines. Few medicines carry warning labels cautioning people to avoid consuming grapefruit juice while taking the drugs in order to avoid an accidental overdose.

**Nitrogen Compounds**

**Alkaloids** - another large class of bitter-tasting nitrogenous compounds found in many vascular plants and include caffeine, cocaine, morphine, and nicotine. They are the derivatives of amino acids namely aspartate, lysine, tyrosine, and tryptophan, having powerful effects on animal physiology. **Caffeine** is an alkaloid found in plants such as coffee (*Coffea arabica*), tea (*Camellia sinensis*), and cocoa (*Theobroma cacao*) which are toxic to both insects and fungi. Infact, high levels of caffeine produced by coffee seedlings can even inhibit the germination of other seeds in the vicinity of the growing plants, a phenomenon called **allelopathy**(allelopathy allows one plant species to defend itself against other plants that may compete for nutrient resources and growing space).

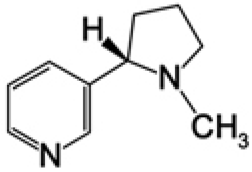

Figure 17. Nicotine

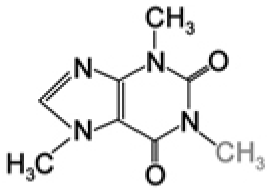

Figure 18. Caffeine

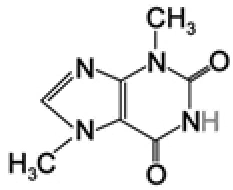

Figure 19. Theobromine

Members of the *Solanaceae* family producing many important alkaloid compounds. **Nicotine** is an alkaloid that is produced in the roots of *Nicotiana tabacum* (tobacco) and transported to leaves where it is stored in vacuoles. It is released when herbivores graze on the leaves and break open the vacuoles. **Atropine** is a neurotoxin and cardiac stimulant produced by the deadly nightshade plant (*Atropa belladonna*). Although it is toxic in large quantities, it has been used by humans medicinally in small amounts as a pupil dilator and antidote for some nerve gas poisonings. **Capsaicin** and related **capsaicinoids** produced by members of the genus *Capsicum* are the active components of chili peppers and produce the characteristic burning sensation in hot, spicy foods.

**Cyanogenic glycosides** are a particularly toxic class of nitrogenous compounds that break down to produce **hydrogen cyanide** (HCN), a lethal chemical that halts cellular respiration in aerobic organisms. Plants that produce cyanogenic glycosides also produce enzymes that convert these compounds into hydrogen cyanide, including glycosidases and hydroxynitrile lyases, but they are stored in separate compartments or tissues within the plant; when herbivores feed on these tissues, the enzymes and substrates mix and produce lethal hydrogen cyanide. **Glucosinolates**, also known as mustard oil glycosides, are sulfur-containing compounds synthesized by members of the mustard family (*Brassicaceae*) and produce cyanide gas when broken down by enzymes called **thioglucosidases**.

**Proteins and Enzymes**

Numerous plants and seeds contain such proteins that specifically inhibit pathogen and pest enzymes. They form complexes that block active sites or alter enzyme conformations, ultimately reducing enzyme function. These proteins are generally small and rich in the amino acid cysteine. They include defensins, amylase inhibitors, lectins, and proteinase inhibitors. Once activated upon attack by pathogen or pest to the plant, defensive proteins and enzymes effectively inhibit fungi, bacteria, nematodes, and insect herbivores.

**Defensins** are small cysteine-rich proteins that display broad anti-microbial activity and were first isolated from the endosperm of barley (Hordeum vulgare) and wheat (Triticum aestivum). They are widely distributed and may be present in most plants. Defensins are best characterized in seeds, but can be found in virtually all types of plant tissues including leaves, pods, tubers, fruit, roots, bark, and floral tissues. Their wide range of biological activities serve to inhibit the growth of many fungi and bacteria. Some defensins also inhibit digestive proteins in herbivores. The precise mechanisms employed by plant defensins to inhibit fungi and bacteria are still being characterized, but they appear to act upon molecular targets in the plasma membrane of pathogens. These defensins may inhibit pre-existing ion channels or form new membrane pores that disrupt cellular ion balance.

**Digestive enzyme inhibitors** are proteins which block the normal digestion and absorption of nutrients by vertebrate and invertebrate herbivores. Alpha-amylase inhibitors are proteins commonly found in legumes that bind to amylase enzymes and inhibit starch digestion. Lectins are non-enzymatic proteins and glycoproteins that bind to carbohydrates and exhibit a wide range of functions including disruption of digestion in insects and agglutination of blood cells in vertebrates. Ricin is a powerful toxin produced in castor beans (Ricinus communis). It combines a lectin molecule with an N-glycoside hydrolase that enters animal cells and inhibits protein synthesis. Ricin is a highly potent toxin, having an average lethal dose of only 0.2 milligrams in humans.

**Protease inhibitors** are typically produced in response to herbivore attack and inhibit digestive enzymes including trypsin and chymotrypsin. They have been well studied in legumes, solanaceous plants, and grasses. Herbivore feeding often triggers a series of molecular signaling events that induce systemic production of these compounds in distal tissues that contribute to the protection of undamaged plant parts from subsequent attacks by a wide range of herbivore pests.

In response to pathogens**,** few plants produce **Hydrolytic enzymes** which accumulate in extracellular spaces where they degrade the cell walls of pathogenic fungi. **Chitinases** are enzymes that catalyze the degradation of **chitin**, a polymer with a backbone similar to cellulose that is present in the cell walls of true fungi. **Glucanases** are enzymes that catalyze the degradation of glycosidic linkages in **glucans**, a class of polymers similar to cellulose that is present in the cell walls of many oomycetes (water molds). In vitro analysis has verified the anti-fungal properties of these compounds, and transgenic plants expressing high levels of these enzymes exhibit increased resistance to a wide range of both foliar and root pathogens. Bacterial cell walls are effectively degraded by hydrolytic enzymes called **Lysozymes**.

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