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Pathogen Penetration into the Host Plant Tissues Challenges and Obstacles – An Overview

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Abstract: Varieties of mechanisms have been developed by plants to adapt, cope with, defend and ward off different arrays of invasion; this includes aggressive invasions from pathogenic organisms that cause diseases. The plant upon sensing danger activates certain signaling pathways within them, this leads to the induced gene expressions with different defensive roles. Their system that activates immunity within and the ability to detect microbial pathogens will be presented. For an infection to occur there must be a close ecological relationship that will be established between the host plants and the pathogens. Attention is also drawn to how pathogens produce plant penetrating mechanisms to invade and bring down the plants defensive structures and the various types of plant pathogens that invade host plants. This paper also reviews the current knowledge of defense mechanisms in host plants among which includes cell wall fortification, defense genes and its activation, secondary metabolites synthesis and defense hormones generation. Resistance and defense can be manipulated to develop varieties of crops which easily fight and inhibit infectious pathogenic stress, as it can also be used as a part of integrated disease management for productive crop production. The knowledge derived from this work together with other research studies in this area will help to draw highlight on the major components in plant defense responses and to design strategies to enhance resistance to pathogen invasion in plants.
Keywords: Host plants, plant mechanisms, pathogen penetration, defense genes, immunity

INTRODUCTION

Plants and micro-organisms have long been in existence, as plants are the building block of living things, supplying food to man and micro-organisms. There is a total dependence of humans on plants for food and other important products that is derived from plants. They include materials for cosmetics, soap, plastics, wood, textiles, dyes, medicines, inks, rubbers and chemicals for industries. Several organisms which include protists, insects, fungi, bacteria, and vertebrates derive its nutrients also from plants. To ward off these pathogens, plants must recognize the invaders and activate fast and effective defense mechanisms that arrest the pathogen. Perception of the pathogens is central to the activation of a successful plant defense response Ines and Marcos, 2013 [1].

Even though plants do not have the exact immune systems like that of animals, still they have developed multiple, unique structural, chemical, and protein-based defenses designed to detect invading organisms and stop them before they are able to cause extensive damage, in the same way plant pathogens have made many adaptations to enable them to invade plants, overcome plant defense mechanisms, and colonize plant tissues for growth survival, and reproduction [2-6].

There is an extensive use of various strategies use by plant pathogens. Pathogenic bacteria increases rapidly in spaces within the cells known as the apoplast, they enter via gas or water pores that is, the stomata and hydathodes respectively, or access entry through wounds. Nematodes and aphids feed by inserting a stylet directly into a plant cell. Fungi can directly enter plant epidermal cells, or extend hyphae on top of, between, or through plant cells. Pathogenic and symbiotic fungi and oomycetes can invaginate feeding structures (haustoria), into the host cell plasma membrane. Haustorial plasma membranes, the extracellular matrix, and host plasma membranes form an intimate interface at which the outcome of the interaction is determined. These diverse pathogen classes all deliver effector molecules (virulence factors) into the plant cell to enhance microbial fitness [7].

When the pathogens get established in the plant, they temporarily avert competitions from organism and saprophytes in the soil and on host plant surfaces. So before any pathogen can infect a plant, it must gain access into the plant, gather nutrients from it, and neutralize its defensive mechanisms. Pathogens accomplish these activities mostly through secretions of chemical substances that affect certain components or metabolic mechanisms of their hosts. Penetration and invasion, seems to be promoted by or in some cases be entirely the result of, the mechanical force exerted by certain pathogens on the cell walls of the plant [2]. Whatever the kind of defense or resistance a host plant employs against a pathogen or against an agent, it is ultimately controlled, directly or indirectly by the genetic materials (genes) of the host plant and of the pathogen [1].

TYPES OF PLANT PATHOGENS

BIOTROPHS:

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 and 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* [2]. The relationship between a biotroph and its plant host is highly specialized as well as structurally and biochemically complex. Obligate biotrophs penetrate the host cell wall, colonizing the intercellular space using feeding structures such as haustoria to absorb nutrients and suppress host defenses without disrupting the plasma membrane [8, 9]. Kristin Laluk *et al*., 2010)

NECROTROPHS:

Some other pathogens often produce toxins or tissue-degrading enzymes that overwhelm plant defenses and promote 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* [2].

Necrotrophic pathogens are bacterial, fungal and oomycete species that have very destructive pathogenesis strategies resulting in extensive necrosis, tissue maceration, and plant rots. To cause disease, necrotrophs secrete disease agents including Phytotoxins, cell wall degrading enzymes (CWDEs), and other extracellular enzymes into host tissue both prior to and during colonization, with primary infection involving the formation of expanding necrotic lesions [10, 11]. Kristin Laluk *et al*., 2010)

HEMIBIOTROPHS:

It has been noted that certain pathogens which are biotrophic at the onset of early infection but later metamorphises to become necrotrophic at the latter stage of the disease infection. These pathogens are known as hemibiotrophs. Examples include *Magnaporthegrisea*, rice blast disease causing fungus (Doughari, 2015)

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 is capable of causing 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 harbor 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 for instance cultivar Rio Grande, are capable of recognizing the bacteria and limiting disease via resistance (an incompatible response). Disease resistance exists as a continuum of responses ranging from immunity (the complete lack of any disease symptoms) to highly resistant (some disease symptoms) to highly susceptible (significant disease symptoms) [2].

PATHOGEN INVASION

(a) Mechanical forces exerted on host tissues by pathogens

Insects are vectors that transmits viruses into plants, therefore there is no mechanical force exerted by them. Certain fungi usually apply mechanical forces on the plant they are to invasion. When fungus lands on a plant surface, and contact is established, diameter of the tip of the hypha or radical in contact with the host increases and forms the flattened, bulb-like structure called the appressorium. This increases the area of adherence between the two organisms and securely fastens the pathogen to the plant. From the appressorium, a fine growing point, called the penetration peg arises and advances into and through the cuticle and the cell wall Richard, 2013 [1].

(b) Chemical weapons of pathogens

Although some pathogens may use mechanical force to penetrate plant tissues, the activities of pathogens in plant are largely chemical in nature. Therefore, the effects caused by pathogens on plants are almost entirely the result of biochemical reactions taking place between substances secreted by the pathogen and those present in or produced by the plant.

The main groups of substances secreted by pathogens in plants that seem to be involved in production of disease, either directly or indirectly, are (1) Enzymes, (2) Toxins, (3)Growth regulators, (4)Polysaccharides (plugging substances).

The enzymes include lipases and cutinizes for breaching the wax and cuticle of aerial parts of the plant as well as enzymes for degrading cell-wall constituents such as pectic substances, cellulose and lignin Richard, 2003 [1].

Generally, plant pathogenic enzymes breakdown the structural constituents of host cells, disintegrate intercellular inert food substances, has effects on its membranous components and the protoplast, thereby interferes with its systems. Toxins adversely affects the cell protoplast components, interfere with its membranous permeability and functions. Growth regulatory hormones also affect the cells causing them to increase or decrease in its ability to divide and enlarge. Polysaccharides work directly in the vascular diseases, where they passively interrupt water translocation in plants.

Plants Immune System

The plant immune system consists of two interconnected tiers of receptors, one outside and one inside the cell. Both systems sense the intruder, respond to the intrusion and optionally signal to the rest of the plant and sometimes to neighboring plants that the intruder is present. The two systems detect different types of pathogen molecules and classes of plant receptor proteins (Wikipedia). The first branch recognizes and responds to molecules common to many classes of microbes, including non-pathogens. The second responds to pathogen virulence factors, either directly or through their effects on host targets [12]. One uses transmembrane pattern recognition receptors (PRRs) that respond to slowly evolving microbial- or pathogen-associated molecular patterns (MAMPS or PAMPs), such as flagellin [13]. The second acts largely inside the cell, using the polymorphic NB-LRR protein products encoded by most R genes (Dangl and Jones, 2001; [13].

Microbial Pathogens Detection and pre-existing structural line of defenses

Several arrays of complicated mechanisms used for surveillance have been developed by plants that detect potential deadly pathogens, they quickly respond before these organisms can cause severe damage. These surveillance systems are linked to specific pre-programmed defense responses. Basal resistance, also called innate immunity, is the first line of pre-formed and inducible defenses that protect plants against entire groups of pathogens. Basal resistance can be triggered when plant cells recognize microbe-associated molecular patterns (MAMPs) including specific proteins, lipopolysaccharides, and cell wall components commonly found in microbes [2]. This means that living plant cells gets fortified against invasion. Pathogens and non-pathogens can trigger basal resistance in plants as a result of the presence of these molecular components in their cells. Plants are able to recognize MAMPs through pattern recognition receptors that specifically bind to their target MAMP, and recognition leads to activation of the plant's basal immune response [13]. MAMP detection leads to a signal transduction and amplification kinase cascade that triggers the activation of pathogenesis related (PR) proteins [14] the production of reactive oxygen species (ROS) [15, 16] and several secondary metabolites, which includes callose deposition that act as a physical and chemical defense against pathogen invasion.

Pathogens keep developing countermeasures so as to defeat basal resistance in some plant species. In response to pathogen evolving mechanisms to suppress basal defense, plants do also bring up other defensive line, known as the hypersensitive response (HR). The HR 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. Bacteria, fungi, viruses, and microscopic worms called nematodes are capable of inducing the HR in plants [2]. Upon triggering the hypersensitive response, tissues in the plant may establish high resistance to broad range of pathogens for a long time period. This phenomenon is known as systemic acquired resistance (SAR) and it stand for a heightened state of readiness wherein plant resources gets fortified in the case of further invasion from pathogens. Phenotypically, systemic resistance is manifested as a protection of the plant not only against the invasioning pathogen, but also against other types of pathogens. Although some specificity has recently been described, the resistance seems to be rather non-specific and long-lasting [6]. Researches have been carried out on some model species [17, 18] and some researchers also have learned to trigger SAR artificially by using plant activators chemicals to spray on plants. These substances are been accepted in the agricultural market because they are less toxic to wildlife and humans than fungicides or antibiotics.

Another means of plants defense against viruses, in addition to hypersensitive reaction is through a sophisticated genetically defensive mechanism known as RNA Silencing. As viruses replicate in host cells, they produce double-stranded RNA or DNA. Plants can recognize these foreign molecules and respond by digesting the genetic strands into useless fragments and halting the infection. Plants that are infected with viruses will 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 invasion by similar viruses, a process analogous to the memory of vertebrate [2].

PLANT DEFENCES

In general, plants defend themselves against pathogens by a combination of weapons from two arsenals: Structural characteristics that acts as physical barriers and inhibit the pathogens from gaining entrance and spreading through the plant and Biochemical reactions that take place in the cells and tissues of the plant and produce substances that are either toxic to the pathogens or create conditions that inhibit growth of the pathogens in the plant.

Broadly speaking, passive defence mechanisms are those that are present before contact with the pathogen, while active defence mechanisms are activated only after pathogen recognition [1, 19]. Wittstock and Gershenzon 2002 These defence mechanisms can also be grouped into two: pre-existing and post-existing (Hammond-Kosack et al., 1997).The pre-existing, preformed, passive or pre-invasive plant defence mechanisms are the innate basal first line immune defence gadgets indigenously constitutive in the plant even pathogen infection and colonization.(Doughari, 2015). To distinguish between pre-existing and induced defences is usually not easy since there can be considerable overlap. For example, the size and density of physical barriers such as spines and plant hairs [20] which are commonly considered to function as constitutive defences can also be increased by induction [21]. Kant, 2015

Pre-existing structural barriers
The Plant Cell Wall

Cell wall defense structures involve morphological changes in the cell wall or changes derived from the cell wall of the cell being invaded by the pathogen [1]. Plant tissues contain structural barriers that inhibit pathogen invasion. The plant cuticle and the cell wall inhibit the initiation and spread of infection while also serving as sources of elicitors that trigger induced defenses (Kristin Laluk et al., 2010)The cell wall is still the first line of defense against invading pathogens [22, 23] providing excellent structural barrier that also incorporates and activates varieties of chemical defenses upon detecting potential pathogens and its modification is also an important defense mechanism operating in the defense response of flowering plants against necrotrophs [24, 25]. All plant cells have a primary cell wall, which provides structural support and is 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 micro fibrils, which give strength and flexibility to the wall. The cell wall may also contain two groups of branched polysaccharides: cross-linking glycan's and pectins. Cross-linking glycans include hemicellulose fibers that give the wall strength via cross-linkages with cellulose. Pectins form hydrated gels that help "cement" neighboring 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 and "mushy" have seen these pathogens in action[2].

Lignin is also another cell wall component which provides rigidity to the cell. It is a heterogeneous polymer containing phenolic compounds, and also the primary component of wood. When cell walls are highly lignified, they become impenetrable to pathogens, making it 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 [26].

As the cells continue to grow, proteins and enzymes in the cell wall keep reshaping and fortifying its wall. The epidermal layer. It is the first line of defense against invading pathogens and consists of both specialized and unspecialized cells [2]. Epidermis is the first layer of living host cells that comes in contact with invasioning microbes. Its toughness is as a result of the cellulose polymers, hemicelluloses, lignin mineral substances, polymerized organic compounds, suberin etc., [27]. Potato tubers resistant to Pythium Debaryanum contain higher fibre. Silicon accumulation in epidermal walls provides resistance against fungal invasion. Suberization of epidermis confers protection against plant Xanthomonas axonopodis pv. citri because of broad cuticulate lips covering the stomata (Doughari, 2015) Certain varieties have exhibited functional defence mechanism(cv-Hope) in which tomato open late in the day when moisture on leaf surface has dried and the infection tunes have become nonfunctional [28].

The Cuticle:

The epidermal cells of aerial plant parts are often covered in a waxy cuticle that not only prevents 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 [2].

Guard Cells:

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 (Jones and Dangyl, 2006)

Trichomes: Known as 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. Trichome density negatively affects the ovipositional behavior, feeding and larval nutrition of insect pests [29]. In addition, dense trichomes affect the herbivory mechanically, and interfere with the movement of insects and other arthropods on the plant surface, thereby, reducing their access to leaf epidermis [30]. 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 [2].

Thorns are modified branches that protect plants from grazing vertebrates, and include the honey locust tree (Gleditsiatria canthos). 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 speaking, the "thorns" on the stem of rose plants (Rosas pp.) are neither true thorns nor spines: they are actually outgrowths of the epidermis called prickles [2].

Idioblasts: Also known as "crazy cells", are highly specialized immune plant cells. They help protect plants against herbivory because they contain toxic chemicals or sharp crystals mainly calcium oxalate which tear the mouthparts of insects and mammals as they feed. There are many classes of idioblasts including pigmented cells, sclereids, crystalliferous cells, and silica cells. Pigmented cells often contain bitter-tasting tannins that make plant parts undesirable as a food source (Doughari, 2015). 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 (Urticadioica) 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 that amplify pain receptors in vertebrate animals and increase the sensation of pain (Jones and Dangl 2006; Doughari, 2015)

PRE EXISTING CHEMICAL DEFENSES

As much as structural defenses may provide a plant with different kinds of defense against invading pathogens, yet plant resistance depends much more on biochemical substances which are produced within its cells before or after infection. This happens because a particular pathogen will not infect certain plant varieties even though no structural barriers of any kind seem to be present or to form in these varieties. Similarly, in resistant varieties, the rate of disease development soon slows down, and finally, in the absence of structural defenses, the disease is completely checked.

Moreover, many pathogens that enter non-host plants naturally or that are introduced into nonhost plants artificially, fail to cause infection, although no apparent visible host structures inhibit them from doing so. These examples suggest that defense mechanisms of a chemical rather than a structural nature are responsible for the resistance to infection exhibited by plants against pathogens [1].

Plant Anti-Microbial Secondary Metabolites

- The defensive (secondary) metabolites can be grouped as
- The Phytoanticipins which are stored as inactive forms
- The Phytoalexins which are induced in response to the insect or microbe invasion.
- The phytoanticipins are mainly activated by β-glucosidase during herbivory, which in turn mediate the release of various biocidalaglycone metabolites [31].

The classic examples of phytoanticipins are glucosinolates that are hydrolyzed by myrosinases (endogenous β-thio glucoside Gluco hydrolases) during tissue disruption. Examples of phytoanticipins are Benzoxazinoids (BXs), which are widely distributed among Poaceae. Examples of phytoalexins are isoflavonoids, terpenoids, alkaloids, etc., that influence the performance and survival of the herbivores [32].

Additionally, Secondary metabolites are more involved with plant defense than growth and reproduction of plants. They usually belong to one of three large chemical classes: terpenoids, phenolic, and alkaloids. The secondary metabolites much more than defending plants do also increase their fitness. Report has it that maize HPR to corn earworm, Helicoverpazea (Boddie) is mainly due to the presence of the secondary metabolites C-glycosyl flavone maysin [2"- O - a –Lrhamnosyl- 6- C - (6-deoxy- xylo -hexos-4-ulosyl) luteolin] and the phenylpropanoid product, chlorogenic acid [33].

Terpenoids (terpenes) occur in all plants and represent the largest class of secondary metabolites with over 22,000 compounds described. The simplest terpenoid is the hydrocarbon isoprene (C5H8), a volatile gas emitted during photosynthesis in large quantities by leaves that may protect cell membranes from damage caused by high temperature or light [2].

Terpenoids such as of the monoterpenoids and sesquiterpenoids which are primary components of essential oils are highly volatile compounds that contribute to the fragrance (essence) of plants that produce them. Essential oils often function as insect toxins and many protect against fungal or bacterial invasion. Mint plants (Mentha Spp.) produce large quantities of the monoterpenoids menthol and menthone which are produced and stored in glandular trichomes on the epidermis. Examples of such terpenoids and their sources include peppermint and spearmint (Mentha spp.), basil (Occimum spp.), oregano (Origanum spp.), rosemary (Rosmarinus spp.), sage (Salvia spp.), savory (Satureja spp.), thyme (Thymus spp.), black pepper (Piper spp), cinnamon (Cinnamomum spp), and bay leaf (Laurus spp) [26].

Pyrethrins are monoterpenoid esters produced by chrysanthemum plants that act as insect neurotoxins. Many commercially available insecticides are actually 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 sharp odor [34, 2].

Monoterpenoids are not just used as insecticides. Many spices, seasonings, condiments, and perfumes are made using essential oils that function as insect toxins in plants but are relatively harmless to humans. Examples include peppermint and spearmint (Mentha spp.), basil (Occimum spp.), oregano (Origanum spp.), rosemary (Rosmarinus spp.), sage (Salvia spp.), savory (Saturejas pp.), thyme (Thymus spp.), black pepper (Piper spp.), cinnamon (Cinnamomum spp.), and bay leaf (Laurus spp.) [2]. Gossypol which is also a Diterpenoids produced by cotton (Gossypium hirsutum) possess 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. When produced by plants such as spinach (Spinaciaoleracea), 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 in the United States due to its low toxicity in humans and biodegradable properties.(Jones and Dangl, 2006)

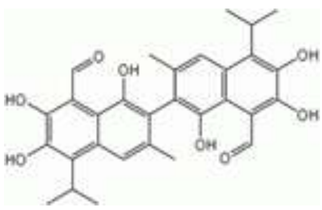

Fig 1: Gossypol

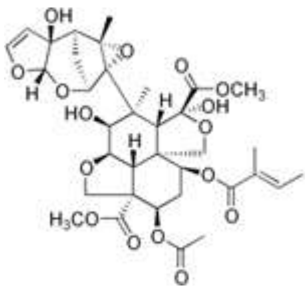

Fig 2: Azadirachtin

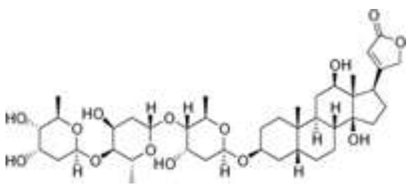

Fig 3: Digoxin [2]

Triterpenoids such as cardiac glycosides are highly toxic to vertebrate herbivores, including humans, if ingested in high amount, can cause heart invasion. Foxglove (Digitalis purpurea) is the major source of the cardiac glycosides digitoxin and digoxin, it is used to treat people with heart diseases in small quantity.

Saponins are glycosylated triterpenoids (triterpenoids with attached sugar groups) that are present in the cell membranes of many plant species. These substances have detergent (soap-like) properties and 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: Botrytis cinerea, Fusarium oxysporum, and Septoria lycopersici are all capable of degrading saponins and causing disease in susceptible saponin-producing plants [2].

Phenolics

Phenolics make up one of the most common and widely known group of defensive compounds, defends against herbivory including insects [35-37].

Phenols act as a defensive mechanism not only against herbivores, but also against microorganisms and competing plants. Qualitative and quantitative alterations in phenols and elevation in activities of oxidative enzyme in response to insect invasion is a general phenomenon [38, 36]. Primarily produced through the shikimic acid and malonic acid pathways in plants, it encompasses varieties of defense-related compounds among which are flavonoids, tannins, and lignin, anthocyanins, phytoalexins, and furano coumarins.

Flavonoids are one of the largest classes of phenolics that defend plants against a variety of biotic and abiotic stresses which includes pathogens, insect pests and UV radiations [39]. Anthocyanins are colorful water-soluble flavonoids pigments produced by plants to protect foliage from the damaging effects of ultraviolet radiation. Anthocyanins are responsible for the showy colors of many plants and are present in high concentrations in flowers, fruits, and the leaves of deciduous plants in fall.

Phytoalexins are isoflavonoids with antibiotic and antifungal properties that are produced in response to pathogen invasion. 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.

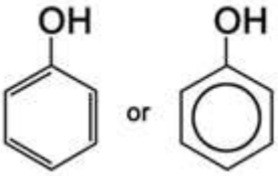

Fig 4: Phenol, the simplest phenolic compound

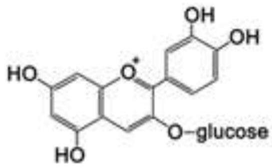

Fig 5: Cyanine glycoside, an anthocyanin

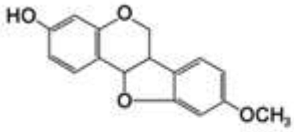

Fig 6: Medicarpin, a phytoalexins [2]

Tannins are water-soluble flavonoid polymers produced by plants and stored in vacuoles. They have a strong toxic effect on phytophagous insects, affecting their growth and development by binding to the proteins, reduce nutrient absorption efficiency, and cause midgut lesions [37]. Lignin is a highly branched heterogeneous polymer found principally in the secondary cell walls of plants, although primary walls can also become lignified. It consists of hundreds or thousands of phenolic monomers and is a primary component of wood. Because it is insoluble, rigid, and virtually indigestible, lignin provides an excellent physical barrier against pathogen invasion. Furano coumarins are phenolic compounds produced by a wide variety of plants in response to pathogen or herbivore invasion. They are activated by ultraviolet light and can be highly toxic to certain vertebrate and invertebrate herbivores due to their integration into DNA, which contributes to rapid cell death [2].

Nitrogen Compounds

Alkaloids are a large class of bitter-tasting nitrogenous compounds that are found in many vascular plants and include caffeine, cocaine, morphine, and nicotine. They are derived from the amino acids aspartate, lysine, tyrosine, and tryptophan, and many of these substances have powerful effects on animal physiology. Caffeine is an alkaloid found in plants such as coffee (Coffea arabica), tea (Camellia sinensis), and cocoa (Theobroma cacao). It is toxic to both insects and fungi. In fact, 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 growing space and nutrient resources.

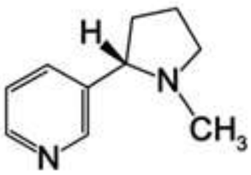

Fig 7: Nicotine

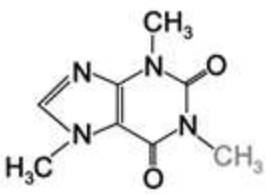

Fig 8: Caffeine

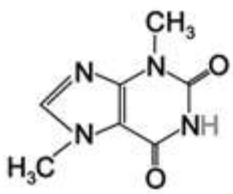

Fig 9: Theobromine [2]

Members of the nightshade family (Solanaceae) produce many important alkaloid compounds.

Nicotine is an alkaloid that is produced in the roots of tobacco plants (Nicotiana tabacum) and transported to leaves where it is stored in vacuoles. It is released when herbivores graze on the leaves and break open the vacuoles Brown Guest, 1980; [2, 34]. 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 medicinally by humans 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 their characteristic burning sensation in hot, spicy foods.

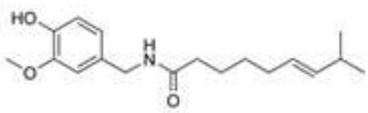

Fig 10: Capsaicin

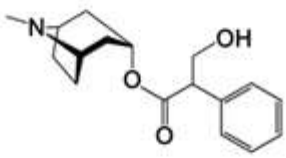

Fig 11: Atropine

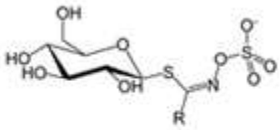

Fig 12: Glucosinolates[2]

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 glycosidase and hydroxy nitrilelyases, 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 [2, 22].

Plant defensive proteins and Enzymes

Certain proteins are contained in plants and seeds that specifically stop pathogen and pest enzymes, they block their active sites or alter enzyme conformations by formation of complexes, thereby reducing their enzymatic function. They are defensins, amylase inhibitors, lectins, and proteinase inhibitors. Proteins need plant resources and energy in high amount to produce unlike simple chemicals such as terpenoids, phenolics, and alkaloids; therefore, many defensive proteins are only produced in significant quantities only when a pathogen or pest has invaded the plant.

Defensive proteins and enzymes upon activation can effectively inhibit fungi, bacteria, nematodes, and insect herbivores. Lectins are carbohydrate-binding (glyco) proteins, ubiquitous in nature, and possess protective power against a range of pests [40, 41]. The insecticidal activities of different plant lectins have been utilized as naturally occurring insecticides against insect pests [42].

One of the most important properties of lectins is their survival in the digestive system of herbivores that gives them a strong insecticidal potential [41]. They act as antinutritive and/or toxic substances by binding to membrane glycosyl groups lining the digestive tract, leading to an array of harmful systemic reactions. Lectins are stable over a large range of pH and damage the luminal epithelial membranes, thereby interfere with the nutrient digestion and absorption. Disruption of lipid, carbohydrate, and protein metabolism causes enlargement and/or atrophy of key tissues, which in turn alters the hormonal and immunological status, threatening the growth and development of insects [40-42].

Protease inhibitors are typically produced in response to herbivore invasion and inhibit digestive enzymes including trypsin and chymotrypsin. They occur widely in nature but have been well studied in legumes, solanaceous plants, and grasses [2].

Higher concentration of PIs occurs in storage organs such as seeds and tubers, and 1 to 10% of their total proteins comprise of PIs, which inhibit different types of enzymes and play an important role in plant defense against insect herbivory [43, 44]. PIs bind to the digestive enzymes in the insect gut and inhibit their activity, thereby reduce protein digestion, resulting in the shortage of amino acids, and slow development and/or starvation of the insects [45]. The defensive function of many PIs against insect pests, directly or by expression in transgenic plants to improve plant resistance against insects has been studied against many lepidopteran [4, 46]. For example, serines PIs have a primary role in defence [47] and affect the performance of some lepidopteran species [48]. Yeh et al., 1997.

Small cysteine-rich defence proteins

There are two families of small cysteine-rich proteins that are suggested to play a role in plant defence against herbivores: defensins (e.g. PR-12) and cyclotides.

Defensins are small cysteine-rich proteins, commonly synthesized in plants but also by animals. They are proteins of 45–54 amino acids that contain eight conserved cysteine residues and are similar to thionins [49]. Most defensins operate by binding to cell membranes, resulting in pore-like membrane defects, causing efflux of essential ions and nutrients. Plant defensins are predominantly active against fungi [50] but some defensins inhibit α-amylase activity and have no effect on fungi [51, 52].

Hydrolytic enzymes: Responding to pathogens invasion, some plants produce enzymes, and they are stored in extracellular spaces, from there, they degrade pathogenic fungi cell wall.

They include:
Chitinases: They catalyze the breakdown of chitin, a polymer with a backbone similar to cellulose, present in true fungi's cell walls. 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. Lysozymes are hydrolytic enzymes that are capable of degrading bacterial cell walls [2].

Defense Trough Lack of Essential Factors

Lack of Recognition between Host and Pathogen. A plant species either is a host for a particular pathogen, e.g., wheat for the wheat stem rust fungus or it is not a host for that pathogen, e.g., tomato for wheat stem rust fungus. How does a pathogen recognize that the plant with which it comes in contact is a host or non-host plants of a species or variety may not become infected by a pathogen if their surface cells lack specific recognition factors (specific molecules or structures) that can be recognized by the pathogen? If the pathogen does not recognize the plant as one of its host plants, it may not become attached to the plant or may not produce infectin substances, such as enzymes, or structures, such as appressoria, penetration pegs, and haustoria, necessary for the establishment of infection [1].

Defense through Hypersensitivity

Hypersensitivity acts as a defense mechanism in plants against pathogens. This reaction occurs only in incompatible host-parasite combinations. As a result of this reaction, the inactivation and localization of the pathogen takes place resulting in the death of the infected tissue. The further growth of the pathogen is stopped, since the necrosis occurs at the infection site, and the pathogen cannot utilize the dead cells. The hypersensitive reaction starts when the pathogen enters the host and establishes its relationship with physiological activities of the host plant [53].

CONCLUSION

In these times of food scarcity, it is so important to extensively study the causes of plant pest and diseases and research on the best methods of control. The knowledge of how plants are invasioned by pathogenic parasites will suitably arm the pathologists with the best arsenals to combat against the invasion. Even though plants have its own defensive mechanisms, they also need external tools by which they will fight better, and this is the essence of this study. A proper understanding of the plant cell signaling mechanisms, the different roles hormones play in disease resistance is needful for adoption of a good control of plant diseases.

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