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Enzymes Secreted by Phytopathogenic Fungi to Infect Plant Tissues

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Abstract The world's most dangerous plant illnesses are brought on by phytopathogenic fungi, which may cause a major negative effect on crop yields in large-scale agricultural production. Fungi are among the most common causes of plant disease. Pathogenic fungi use a variety of strategies to invade plants and cause disease. While some fungi live inside living tissue (biotrophs), others kill their hosts and feed on dead materials (necrotrophs). The complex structure of the plant cell wall functions as a mechanical barrier, restricting most diseases from entering the plant. To penetrate the host and cause disease, phytopathogenic fungi must secrete several hydrolytic enzymes that break down complex polysaccharides in the plant cell wall. Various types of cell wall-degrading enzymes, such as cutinases, cellulases, hemicellulases, lignases, lipases, pectinases, and proteinases, are produced by fungi during infection. The most significant cell wall-degrading enzymes during infection that have been described in plant pathogenic fungus species and are crucial to the formation of a successful infection are compiled in this review.

Keywords cell wall-degrading enzymes, plant cell wall, plant pathogenic fungi

1. Introduction

Plants are the most prevalent and important group of autotrophic organisms. All heterotrophic organisms, including microorganisms, insects, and animals depend on their abundant organic material for nourishment. The main component of the ecosystem, plants affect human life directly or indirectly. Numerous biotic agents, such as pathogens and herbivorous insects, attack plants in nature, and their impacts can be devastating for the host plants [1]. Plant diseases are mostly caused by pathogens such as viruses, nematodes, bacteria, and fungi [2]. Plant diseases affect crop yield, food quality, and global food security in agroecosystems [3]. An estimated 10–16% of the world's crop production is lost each year due to plant diseases, with with hundreds of billions of dollars in direct economic losses [4-6]. One of the most damaging plant parasites are phytopathogenic fungi, which can lead to major crop yield losses as well as serious disease, and fungi are responsible for 70-80% of plant disease[6].

Plant pathogens are categorized into three groups depending on their feeding habits: biotrophs, necrotrophs, and hemibiotrophs [7-9]. Necrotrophs feed on the host cell after it has been killed, whereas biotrophs obtain nutrients from living cells by preserving the vitality of their host. Third-group hemibiotrophs exhibit both types of nutrition by transitioning from an early biotrophic phase to a later necrotrophy. Hemibiotrophic pathogens exhibit great variation in the duration of their biotrophic or necrotrophic phase [8]. All the three modes of pathogenesis have been identified in fungi. Specific infection structures are developed by plant pathogenic fungi, who display a variety of infection techniques in order to obtain nutrients.

Using feeding structures such as haustoria, appressoria, and hyphae (Figure 1), biotrophic fungi penetrate the plant cell wall and colonize the intercellular space, allowing them to collect nutrients and suppress the plant's

defense mechanisms [10,11]. Instead of producing specific infection structures, necrotrophs, on the other hand, overpower the host by employing a range of secreted pathogenicity and virulence factors during infection [8].

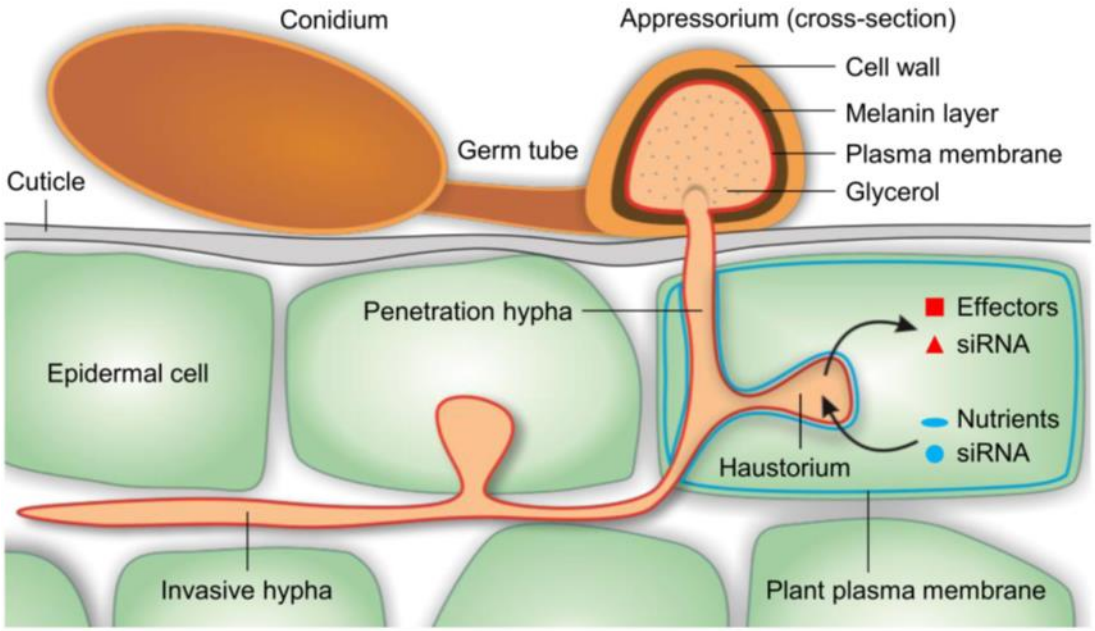

Figure 1. Using unique nutritional structures, fungi penetrate the cell walls of plants to inhabit the intercellular space [12].

Plant cell walls are a naturally occurring nanoscale network structure composed primarily of polysaccharide polymers like cellulose, hemicellulose, and pectin, but also including lignin and glycoproteins [13,14]. The primary and most important barrier to disease penetration is the plant cell wall, which is covered with cuticles. Fungal pathogens may penetrate the plant directly by secreting hydrolytic enzymes, or may be penetrated through stomata or other natural openings or from a physically injured tissue [15].
Cell wall-degrading enzymes (CWDEs) are extracellular hydrolytic enzymes secreted by many phytopathogenic fungi that help in the infection process. Through the degradation of cuticle, wax, and cell walls, they can contribute to tissue invasion and the spread of pathogens, so contributing to disease. Additionally, they have the ability for eliciting a host defense response [11,13,16].

2. Plant cell wall-degrading enzymes

Phytopathogenic fungi release a diverse range of CWDEs, including cellulases, cutinases, hemicellulases, lignases, lipases, pectinases, and proteinases, which constitute the focus of this research. These enzymes are required for the degradation of plant cell wall polysaccharides, particularly pectin, hemicellulose, and cellulose.

2.1. Cutinases

Plants, bacteria, and fungi contain cutinases (EC 3.1.1.74), which have a variety of structures and characteristics [17]. Cutinase is identified by its capacity to break degrade cutin, an aliphatic polyester that serves as many plants' natural defense mechanism [18]. The pathogenicity of plant pathogens is mostly associated with natural cutinases, which have the ability to break the cutin barrier and release carbon sources [19,20]. As a preliminary stage in tissue degradation, cutinases break down the cutin on the cuticle layer, presoftening the tissue for mechanical penetration. Cutinases are produced by a number of fungi and at least one species of bacteria, according to studies. Evidence also suggests that cutinases are continuously produced, albeit at low concentrations, and that the degradation products of cutinases frequently cause even greater secretion of the enzyme. Research indicates that the virulence of some organisms may be associated with their production of cutinase. On their aboveground surfaces, such as their stems, leaves, and fruits, most plants have a coating called the cuticle that is made of cutin [21]. A matrix-like structure with waxy components embedded in the layers of carbohydrates forms this layer of cutin. Many fungi that cause plant diseases can manufacture cutinase; Penicillium spinulosum was the first fungus to demonstrate evidence of the enzyme's activity [22]. The cutinase

of the fungus *Nectria haematococca*, which is the perfect form of *Fusarium solani* f. sp. *pisi* and causes foot rot of pea, is one of the best studied cell wall disintegrating enzymes. It has been demonstrated that cutinase plays a key role in enabling the early stages of plant infection. Cutinase makes up 70% of the total extracellular protein released by *N. haematococca* when it is grown *in vitro* on cutin as its only carbon source. Furthermore, it has been proposed that during initial contact between fungal spores and plant surfaces, a trace amount of catalytic cutinase generates cutin monomers, which subsequently up-regulate the expression of the cutinase gene [22]. Cutinase supplementation to fungi that cannot make it naturally has been found to improve fungal infection success rates [22]. Studies have demonstrated that these enzymes have an important role in the pathogen's virulence [23,24].

2.2. Cellulases

The primary polymeric component of plant cell walls, cellulose is the most prevalent polysaccharide on the world and a significant renewable resource. The hardest component of plant cell walls to break down is cellulose [25]. Comprising glucan chains with repeated β(1-4) D-glucose units, it forms microfibrils in lignocellulose found in plant cell walls. Cellulases secreted by pathogens have a function in the softening and disintegration of cell wall components in live plant tissues [26,27]. During the infection and expansion process, *Fusarium graminearum* secretes cell wall-degrading enzymes such as pectinase, xylanase, and cellulase, causing the decomposition of host cell wall components and cell wall relaxation, which is beneficial for pathogen penetration and expansion in host tissue [28]. Endo-cleaving (endoglucanases) and exocleaving (cellobiohydrolases, exocellulases) enzymes acting on cellulose comprise the traditional array of fungal cellulose-degrading enzymes [29]. Based on the type of reaction catalyzed, there are four general categories of cellulases:

Endo-1,4-β-glucanase (EC 3.2.1.4, endocellulase): Numerous wood-rotting basidiomycetes, brown rot and white rot fungi, as well as the plant pathogen *Sclerotium rolfsii* and the basidiomycetous yeast *Rhodotorula* were found to contain endoglucanases. Endoglucanase activity appears to be widespread among basidiomycetes, as evidenced by its detection in cultures of the enzyme in basidiomycetes that decompose litter [30,31], ectomycorrhizal fungi [32,33], and wood-associated yeasts [34].

Cellobiohydrolase (EC 3.2.1.91; exocellulase): A number of white rot basidiomycetes, including the plant pathogen *Sclerotium rolfsii*, have been shown to harbor cellobiohydrolases thus far. Additionally, certain ectomycorrhizal fungi [33,35] and fungi that break down litter [30,31] have been shown to have cellobiohydrolase activity.

β-Glucosidase (EC 3.2.1.21): Most microorganisms manufacture β-glucosidases because cellobiose is a widely available substrate [36]. Enzymes were recovered from many wood-rotting fungi (Basisiomycetes), both white rot and brown rot, the mycorrhizal fungus *Pisolithus tinctorius* and *Tricholoma matsutake*, and the plant pathogen *S. rolfsii*. A few of the wood-associated yeasts couldn't use cellobiose as a substrate, but β-Glycosidases were also isolated from and their activity detected in basidiomycetous yeasts [37,39]. Additionally, pure cultures of litter-decomposing basidiomycetes [30,31] and ectomycorrhizal species [35,40] have been shown to have β-glucosidase activity.

Cellobiose dehydrogenase (EC 1.1.99.18): The extracellular enzyme cellobiose dehydrogenase is produced by ascomycetes and basidiomycetes. First identified in white rot fungi, cellobiose dehydrogenase activity was found to reduction quinones in a cellobiose-dependent manner [41,42], and from *Sporotrichum pulverulentum*, the flavin-containing enzyme cellobiose quinone oxidoreductase was isolated [43].

2.3. Hemicellulases

Because they recycling hemicellulose, a major component of plant polysaccharides, hemicellulolytic microorganisms are important to nature. Plant cell walls are composed of a composite material called cellulose, hemicellulose (which primarily consists of xylan and mannan, galactan, and arabinan), and lignin. Xylan is also thought to be the second most common biopolymer in the kingdom of plants. [44-46]. Hemicellulose, the second most prevalent component of plant cell walls, provides significant cross-linking between cellulose microfibrils [47]. Hemicellulases play an important role in the degradation of plant biomass and carbon transport in nature. Hemicelluloses are a heterogeneous set of branched and linear polysaccharides that are attached to the cellulose microfibrils in the plant cell wall via hydrogen bonds, crosslinking them into a strong network [48]. The complex structure of hemicelluloses needs different enzymes for its complete hydrolysis.

The hemicellulolytic enzymes; Xylanases (EC 3.2.1.8) produce short xylooligomers by hydrolyzing the β-1,4 bond in the xylan backbone. β-Mannanases (EC 3.2.1.78) break down mannan-based hemicelluloses to release short β-1,4-manno-oligomers, which β-mannosidases (EC 3.2.1.25) can then hydrolyze further to produce mannose. α-L-arabinanases (EC 3.2.1.99) and α-L-arabinofuranosidases (EC 3.2.1.55) hydrolyze hemicelluloses that contain arabinofuranosyl. The α-1,2-glycosidic link in the 4-*O*-methyl-D-glucuronic acid sidechain of

xylans is broken by α-D-glucuronidases. The exo-type glycosidases known as β-Xylosidases (EC 3.2.1.37) hydrolyze short xylooligomers into single xylose units. Acetyl xylan esterases (EC 3.1.1.72), which hydrolyze the acetyl substitutions on xylose moieties, and feruloyl esterases (EC 3.1.1.73), which hydrolyze the ester bond between arabinose substitutions and ferulic acid, are examples of hemicellulolytic esterases [46,48].

2.4. Lignases

Lignin, as a key component of the plant cell wall, performs important roles in plant growth and development, as well as serving as a crucial barrier against pests and pathogens [49,50]. Lignin is a phenylpropanoid present in the secondary cell wall and middle lamella of plants. Basidiomycetes, often known as white-rot fungus, are responsible for the majority of lignin degradation. In order to use lignin, these fungi produce ligninolytic enzymes. Laccase, lignin peroxidase, manganese peroxidase, and versatile peroxidase are the major ligninolytic enzymes that play a role in the degradation of lignin, cellulose, hemicellulose, and simiar compounds. The extracellular enzyme laccase (EC 1.10.3.2), which is composed of monomeric, dimeric, and tetrameric glycoproteins, contains copper. This is mostly found in microorganisms, such as actinomycetes, fungi, and bacteria [27,51,52]. Lignin peroxidases (EC 1.11.1.14) are members of the oxidoreductase family, which hydrolyzes lignin and its byproducts when H_2O_2 is present [53]. These are heme-containing enzymes that oxidatively degrade the polymer; they are mostly secreted by higher fungi and certain bacteria [54,55]. The heme-containing enzyme manganese peroxidase (EC 1.11.1.13) is a member of the oxidoreductases family [56]. The solid and liquid form of the enzyme manganese peroxidase is secreted into the microenvironments of ligninolytic microorganisms [57-61]. Versatile peroxidase (EC 1.11.1.16) also known as hybrid peroxidase (manganese-lignin peroxidase) that contains glycoproteins and belongs to oxidoreductase family. Different fungus species, such *Pleurotus*, *Lipista*, and *Bjerkandera*, have been observed to produce peroxidase. [62-66].

2.5. Lipases

Enzymes called lipases (EC 3.1.1.3) catalyze the hydrolysis of various lipid substrates. Lipases have a broad spectrum and can be found in bacteria, fungi, plants, and animals. Their numerous and significant commercial uses are the primary reason for their studies. These enzymes have begun to be recognized as virulence-associated components in microbial plant pathogens, according to a number of recent studies. It is thought that many lipases released by fungal plant pathogens are responsible for the fungi's ability to penetrate plant defenses like cuticles and waxes [67]. The involvement of a secreted lipase in plant virulence was discovered in the fungal pathogen *Botrytis cinerea* [68-70]. This fungal species produces several extracellular hydrolytic enzymes that allow it to immediately penetrate the unharmed plant cuticle and epidermis, resulting in a serious disease that affects grapes. A lipase secreted by the fungal pathogen with a wide host range It has also been established that *Fusarium graminearum* is a virulence factor [71-73]. Pritsch et al.'s [74] observation of sub-cuticular growth of *F. graminearum* following host penetration suggests that lipases may have had a role in some degree in the cuticle's degradation. According to Berto et al. [75], lipase may be crucial for *Alternaria brassicicola* conidia to infect cauliflower leaves. The fungal pea pathogen *Nectria haematococca* has an extracellular lipase known as NhL1, which has been cloned, characterized, and its transcriptional regulation examined [76].

2.6. Pectinases

Among the most prevalent substances found in the primary and middle lamellae are complex polysaccharides called pectin. Additionally, the secondary cell wall has less of it [77]. It has been demonstrated that pectinases are crucial for the infection of some phytopathogenic fungi [78,79]. Pectic enzymes cause cell lysis and plant tissue maceration in addition to altering the structure of the cell wall and making its constituent parts more accessible for other enzymes to break down [80]. Even though pectin doesn't seem to be the most resistant component of cell walls, pectin-degrading enzymes have been shown to be essential to the infection process—as long as pectin degradation weakens cell walls and allows fungi to enter [81]. Fungal pathogens often secrete a variety of extracellular enzymes and may contribute to virulence [82,83]. Pectinolytic enzymes from *B. cinerea* [79], *Aspergillus flavus* [84], *Claviceps purpurea* [85], and *Fusarium* spp. have been reported to have positive effects [86,87]. Several enzymes with pectinolytic activity must work together to degradation pectin [77]. Pectin lyase, pectate lyase, pectin esterase, and polygalacturonase (PGA) are enzymes that degrade peçtin [88,89]. A number of fungi have an expanded family of PGAs, which suggests that they have a high capacity for pectin degradation. These fungi include the necrotrophic white mold fungus *Sclerotinia sclerotiorum*, the gray mold fungus *B. cinerea*, the opportunistic human pathogen *Rhizopus oryzae*, *F. moniliforme*, and *F. oxysporum* f.sp. *melonis* [86,87,90]. The deesterification of pectin into pectate and methanol is catalyzed by pectinesterases. The majority of fungi only have a small number of pectin esterases, which may aid in the degradation of pectin [90].

2.7. Proteinases

Proteases are enzymes that catabolize the breakdown of proteins by hydrolyzing peptide bonds at the post- and translational stages. They are also referred to as peptidases or proteinases. Aspartate, cysteine, metalloproteases, serine, and threonine are the five primary types of proteases that have been identified based on the catalytic residue connected to the attachment to the substrate bond [91]. Proteases found in fungus and bacteria play a crucial part in the recycling of proteins that contain carbon and nitrogen, as well as in the regulation of other cascade processes by means of nutritional signals [92]. Various conditions and ways can be used to manufacture phytopathogenic fungal proteases. Different forms of the same protease can be expressed depending on culture conditions [93]. Numerous phytopathogenic fungus species produce distinct proteases in diverse growth conditions and host tissues [94-96]. Fungal proteases are believed to have a key role in adhesion to host cells, initial plant cell wall penetration, and colonization, among other stages of the infection process [97-100]. For many phytopathogenic fungi, a relationship between the proteolytic activity in the culture media and in the infected plant has been demonstrated to establish disease [101,102]. Additionally, studies on *B. cinerea* cell death conducted by Movahedi and Heale [98] revealed that aspartic protease may be the primary cause of the infection's initial stage. The presence of significant extracellular proteolytic activity in Spunta potato tubers during *F. solani* infection [99] supports the role of proteases in plant hosts as important regulators of infection and immunity-priming factors. The expression of the genes acp1 and asps, which produce acid protease and aspartyl protease, respectively, was revealed during an examination of the genetic underpinnings of proteolytic activity in *S. sclerotiorum* [103]. *Glomerella acutata* produced a wide variety of proteases, including aspartic, cysteine, and serine proteases, demonstrating the role of many proteases in the development of disease [104]. Aspartic proteases have recently been shown to be the key factors of pathogenicity in *B. cinerea* by ten Have et al. [105]. Moreover, mutational experiments in a number of fungal species, including *F. oxysporum*, *Nakataea oryzae*, *Pyrenopeziza brassicae*, *Ustilago maydis*, and *Verticillium dahliae* revealed the necessity of extracellular proteases in phytopathogenicity [100,106-109].

3. Conclusion

Enzymes are a crucial component of fungal plant pathogenesis and participate in both internal and external interactions. The primary structural polysaccharide components of plant cell walls, cellulose, hemicellulose, and pectin, are depolymerized by a wide variety of secreted enzymes that are possessed by the fungi. The clarification of biochemical pathways that may discover new specific targets to protect plants and speed up the development of novel agents for combating plant-pathogenic fungi will be made possible by additional research on the secretion of cell wall-degrading enzymes in various plant-pathogenic fungi.

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