
***Stenocarpella maydis* and *Sporisorium reilianum*: Two Pathogenic Fungi of Maize**

Jorge Alvarez-Cervantes, Edna M. Hernandez-Dominguez,
Maura Tellez-Tellez, Virginia Mandujano-Gonzalez,
Yuridia Mercado-Flores and Gerardo Diaz-Godinez

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Abstract

Stenocarpella maydis and *Sporisorium reilianum* are phytopathogenic fungi that cause white rot in corn cob and head smut in maize (*Zea mays* L.) respectively, diseases that are spread worldwide and cause many economic losses. In this chapter the characteristics of the above diseases, such as their life cycle, pathogenicity factors, control methods, as well as the biotechnological potential of the fungi involved in this processes are described, specifically in connection to their extracellular enzymes.

Keywords: Disease of maize, head smut in corn, *Stenocarpella maydis*, *Sporisorium reilianum*, pathogenicity factors, *Zea mays*

1. Introduction

The crop diseases caused by fungi represent a major obstacle to agriculture worldwide. Corn (*Zea mays* L.) is a crop with a high level of consumption, which is affected by various diseases. *Stenocarpella maydis* and *Sporisorium reilianum* are fungi that generate white rot in corn cob and head smut in maize, respectively, both of which are diseases distributed worldwide causing numerous economic losses [1–4]. *S. reilianum* is a phytopathogen belonging to the order Ustilaginales, which infect a large number of monocotyledonous and dicotyledonous plants. The most outstanding feature of the disease is the presence of carbonous masses of black coloration in the corn cob and maize tassel. This causes excessive deformation and over development, which has been a serious problem since the early 1970s in countries like the United States, Australia, China, South Africa, France, and Mexico [3]. *S. maydis* causes diseases,

and this fungus has a worldwide distribution. The fungus remains latent as mycelium, pycnidia, and spores in crop residues or seeds. The cycle starts from sexual or asexual spores that over-winter on cereal or traces of stubble. The spores are carried by abiotic (wind, rain drops) and biotic (insects, birds) agents towards the maize tassel, where they find the main entrances to the plant; the stigma and damaged, developing grains. The disease is favored when the weather is wet after flowering and when the atmosphere is cool and humid during the grain-filling stage [1]. Currently, control of both fungi has been conducted mainly with the use of resistant hybrids; however, the genotypes that were resistant to the disease in one year may be susceptible in the following season. These fungi produce severe damage to maize cultivation because of their ability to degrade the cell wall components. They do this by excreting enzymes, allowing the infection of, and colonization in, the host plant. Therefore, consideration has been given to the possibility of studying the production and the characteristics of these fungal enzymes, which include xylanases, cellulases, proteases, etc., as well as their associated potential biotechnological applications.

2. Overview of *Sporisorium reilianum* and *Stenocarpella maydis*

2.1. *Sporisorium reilianum*

2.1.1. General characteristics

S. reilianum is a pathogenic basidiomycete, both biotrophic and dimorphic, and is the causal agent of head smut in maize [5–7]. It belongs to the Ustilaginaceae family and was first described as *Ustilago reiliana* (Kühn) and then renamed as *Sphacelotheca reiliana* (Kühn). Studies based on its genetic characteristics allowed it to be placed in the *Sporisorium* genus with two subspecies: *S. reilianum* f. sp. *reilianum* and *S. reilianum* f. sp. *zuae*, affecting sorghum and maize respectively. However, both varieties are able to infect and invade both hosts. *S. reilianum* f. sp. *reilianum*, is highly virulent in sorghum, but does not produce spores on maize, while *S. reilianum* f. sp. *zuae* causes no disease in sorghum with the only recognized symptoms observed being the presence of phytoalexins. Transcriptome analysis of maize leaves colonized by both pathogens showed that most genes are induced with *S. reilianum* f. sp. *zuae* compared with that of *S. reilianum* f. sp. *reilianum*, showing that host specificity is determined by different mechanisms in sorghum and maize [8–9]. This fungus is an inhabitant of the soil where it can survive up to 10 years in the form of a teliospore: a structure generated by fragmentation of the mycelium in plant tissues either on the tassels or in the corn cob. These are semispherical, echinulate, yellowish brown in color but can range from pale to dark red or black (Figure 1). They can be dispersed by rain, wind, wildlife, agricultural machinery, or human beings [5, 10].

The life cycle begins when a dikaryotic young teliospore, suffers karyogamy, giving rise to a spore mature diploid uninucleate. When optimum temperature and humidity conditions are presented, they germinate producing a structure called promycelium, where the nucleus divides by meiosis and the resulting four nuclei pass to lateral cells to form four haploid basidiospores of different sexual compatibility. These can remain in saprophytic manner with

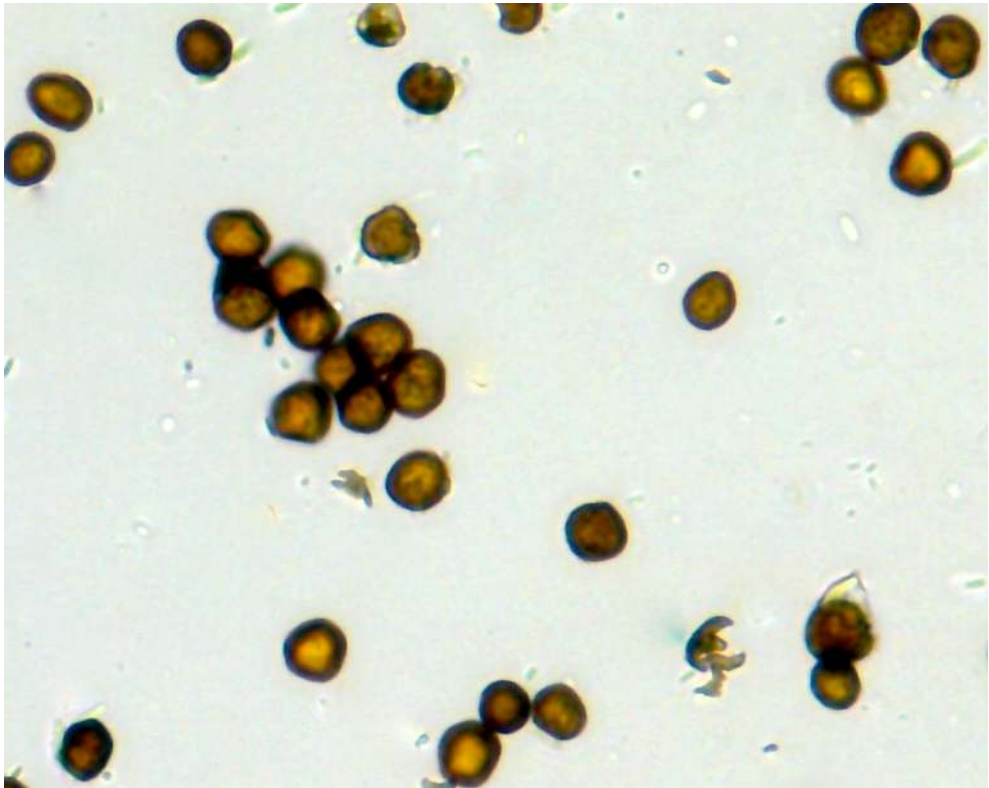


Figure 1. Teliospores of *S. reilianum*. Observation made with a phase contrast microscope at 40X.

their division being by gemmation. It is said that at this point the fungus is in its yeast phase (Figure 2).

When two yeasts with different sexual compatibility (a and b) produce and recognize pheromones, they may come into contact with the young tissues of a plant, forming a complementation tube which allows cell fusion (somatogamy), giving rise to an infective stage which is constituted by a septate dikaryotic mycelium. The formation of an appressorium is crucial for penetration, where the production of lytic enzymes and the mechanical processes of pressure, probably play an important role. In this case the fungus locally degrades the cell wall of the epidermis, permitting penetration and a systemic invasion mainly affecting the undifferentiated reproductive organs, either male or female, of the plant, where the production of teliospores at the time of flowering, are manifested as carbonaceous masses of black coloration on the ears and corn cobs, forming what is commonly known as sori or galls (Figure 3). These structures are bare, unlike common smut caused by *Ustilago maydis* where they are covered by a white membranous tissue with traces of the vascular system of the plant. The stages of the infective diploid and the saprophytic haploid can be maintained in the laboratory, where

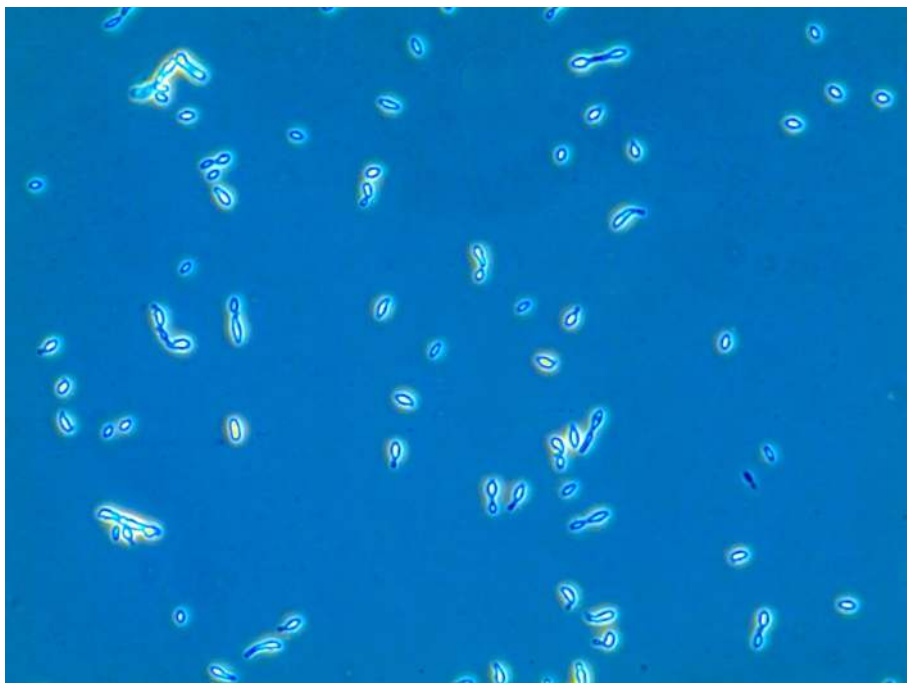


Figure 2. *S. reilianum* in its yeast phase. Observation made with a light microscope at 40X.

reproduction takes place through gemmation. Factors favoring the transition from yeast to mycelium have not been fully described, but may be linked to the temperature, humidity, and pH of the medium [2, 4, 6, 7, 11–14].

The complete genome sequence of *S. reilianum* has already been reported and is deposited in the database at the Munich Information Center for Protein Sequences (MIPS) at the following address; <http://mips.helmholtz-muenchen.de/genre/proj/sporisorium/>, which facilitates research in order to understand the mechanisms that occur during the interaction of the fungus with the plant [3].

2.1.2. Characteristics of the disease

The disease caused by *S. reilianum* called head smut are manifested in the flowering stage due to the presence of a carbonaceous mass of teliospores invading male inflorescences in the tassels replacing pollen formation. The same effect is observed quite frequently in the corn cobs, resulting in the appearance of black soil (Figure 4) [11].

It can be seen that anthocyanin accumulates in stalks, together with the presence of chlorotic spots in the leaves. During colonization an increase of 30% of the total content of auxins in the inflorescences, and a significant accumulation of reactive oxygen species, occurs [4, 11, 14].

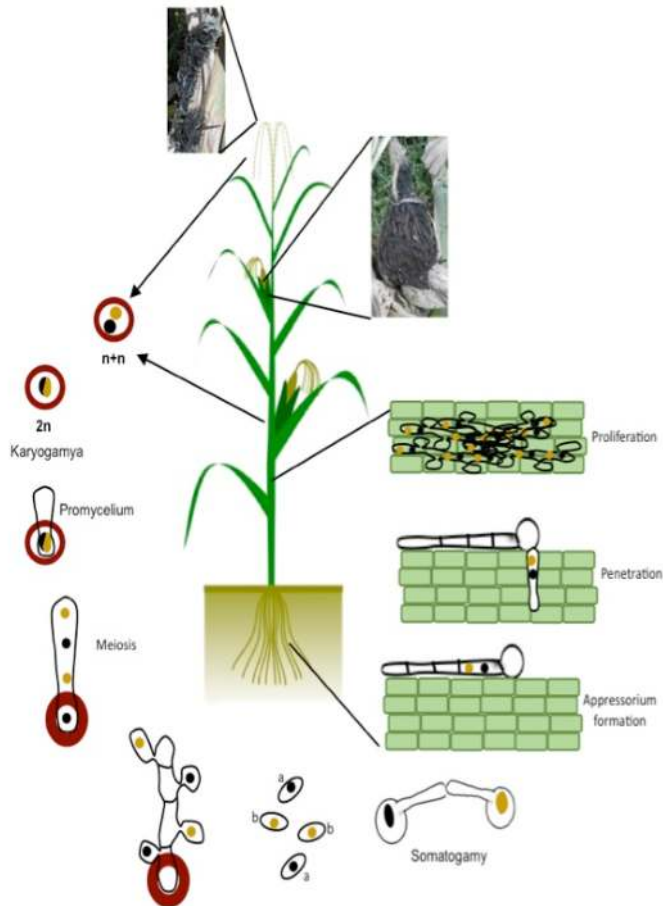


Figure 3. Life cycle of *S. reilianum*. The teliospores are the principal dissemination source. Fungus is heterothallic and homothallic requiring two compatible mating types for sexual reproduction.

The development of the disease is favored when soil moisture is 15–25%, at a temperature of 23–30 °C, with low water potential – the latter has an effect on the transition of basidiospores to hyphae facilitating the fusion of compatible strains, leading to increased disease severity. Nutritional aspects are also important: nitrogen deficiency increases infection, with a lower incidence rate being identified in clay soils than sandy soils [3, 10, 11]. Head smut is not considered as devastating a disease, but still causes severe losses in the crop yields of maize [15–18].

The report for the first specimen was made in 1875 by Kühn, who received the original strain found in Egypt by Dr. Reil in 1868 [19], however, the disease now has a worldwide distribution,

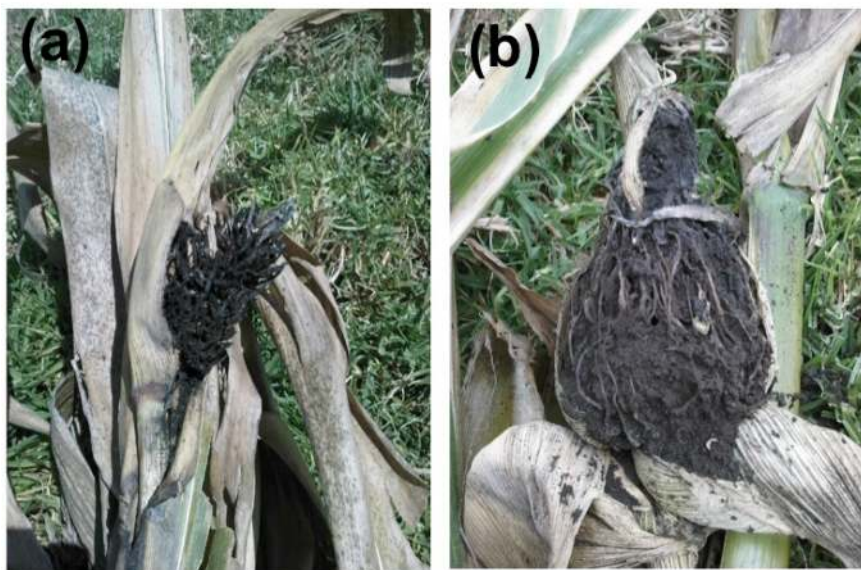


Figure 4. Head smut of maize produced by *S. reilianum* f. sp. *zea*. Presence of a carbonaceous mass of teliospores in the tassel (a) and cob (b).

especially where maize crops are extensively practiced, such as Europe, North, Central, and South America, Africa, Asia, Australia, New Zealand, western India, and Palestine, among other countries [7, 20–23].

2.1.3. Pathogenicity factors

During infection and colonization of *S. reilianum* in the floral tissue of maize, one can identify different interactions, which are described as follows: 1) hyphae and cells of host may be associated and alive; 2) hyphae collapse and cells of host remain alive; 3) hyphae and cells of host collapse; and 4) hyphae is viable and colonizes all cells of the host causing tissue death [2]. This plant pathogen has a high compatibility with its host in order to survive until flowering. During growth within the tissue of maize, hyphae are surrounded by a matrix that allows an area of exchange between the plant and fungus, which is separated from the plasmatic membrane. During this interaction, structures like vesicles are observed that could have the function of endocytosis, which may carry virulence effectors to help with compatibility with the host [24].

The growth of filamentous hyphae in epidermal cells of root, apices, and young tassels of maize, show that the hyphae are mainly in the intercellular spaces and between adjacent epidermal cells, exhibiting no damage to the cell wall of the host, although hyphae are attached to the host. For this plant pathogen, considered biotrophic, intracellular growth is a useful strategy to damage and avoid the response of plant defenses [25].

S. reilianum infection in maize induces a loss of apical dominance showing two modifications in the inflorescences, one of which is the loss of identity of, and the appearance of, phyllodes. These results suggest that the fungus modulates the floral architecture of maize whilst floral genetic regulation could be a secondary consequence of increased reactive oxygen species (ROS) or high levels of auxin, or could also be due to the fact that the fungus regulates floral genetic expression by the secretion of some proteins [4]. Symptoms caused during infection are observed after the floral transition where there are white sori that contain the teliospores, which are formed in the younger part of the panicle, and cause the infected tassels not form floral branches. After flowering, typical smut contains a high amount of teliospores in the infected plant, which allows it to colonize new plants and continue its life cycle [25].

Phytopathogenic fungi have different mechanisms that allow them to penetrate and colonize their hosts. One involves the production, and synergistic action, of extracellular hydrolytic enzymes that degrade the different polymers constituting the cell wall of the plant tissues [26]. The genome sequence of *S. reilianum* shows few genes encoding enzymes that degrade the cell wall [27]. Until now only the hydrolytic activities of aspartyl protease and beta-xylanase, produced in different culture media, have been reported. These enzymes could present an important role during the colonization of the host infection [28, 29].

2.1.4. Strategies for disease control

Because *S. reilianum* infects during germination and in the early stages of plant development, the main strategy to control the disease is the application of fungicides to the seed to prevent the pathogen coming into contact with the host. However, it has been observed that some chemicals can retard plant growth and others reduce seed germination [15, 16, 18, 30]. The application of fungicides to foliar structures has not been found to control the disease [31]. Some chemical agents used to control the disease are: Benlate (benomyl) and carboxin + thiram [32]. Furthermore, fungicides have been used to inhibit the synthesis of ergosterol, among which are triazole and imidazole. Lately, has emerged that azoxystrobin and strobilurin present protection via soil treatment [15, 16, 32-34].

Genetic resistance as an alternative disease control method may be more feasible and economical so development is underway on tolerant maize hybrids with high yields [21]. It has been observed that the use of resistant hybrids to disease in one year may make the next crop susceptible. Crop rotation for legumes, care and cleaning of agricultural machinery, and humidity control, can help reduce the incidence of the disease [35-37].

In recent years, scientists have been looking for new forms of control that also need to be environmentally friendly. One such case is the use of biological controls which represent an alternative for the management of the disease, reducing the use of chemical fungicides [38, 39]. In this respect Mercado-Flores et al. in 2014 applied a native strain of *Bacillus subtilis* to a maize producing area in the Mezquital Valley in the central part of Mexico. It was found that the biological treatment significantly reduced the incidence percentage of smut while increasing maize productivity [37].

2.2. *Stenocarpella maydis*

2.2.1. General characteristics

White rot of stalk and corn cob is a disease caused by the ascomycete *S. maydis*, one of the most destructive worldwide, especially during wet seasons. Symptoms manifest many weeks after infection, affecting roots, stems, and corn cobs, where a white cottony fungal growth is observed in the presence of pycnidia, and the marrow stem is discoloured and disintegrated leaving only the vascular bundles intact – the internodes showing a dark brown coloration. In this case the plant is weakened and easily broken by rain and strong winds. Infected corn grains have less glare and have a dull brown or slightly gray coloration [1, 40, 41].

Natural infection of *S. maydis* on the stem and shank is greater between one to three weeks after pollination, in the presence of rain and temperatures ranging 28–30 °C. Periods of drought before flowering increase the crop's susceptibility to the disease. This occurs mainly in cold regions because conidia lose viability at high temperatures and with exposure to sunlight [1, 40, 42].

S. maydis survives throughout the year between crop residues as pycnidia, which contain the conidia or spores of the fungus (Figure 5). During the wet season, these structures are released and propagated, by splashing rain drops, to the female inflorescences, being deposited around the shank of the corn cob. From there they germinate and penetrate, invading the plant and continuing their life cycle (Figure 6) [43, 44].



Figure 5. Conidia of *S. maydis* with rounded ends and 1–2 septa.

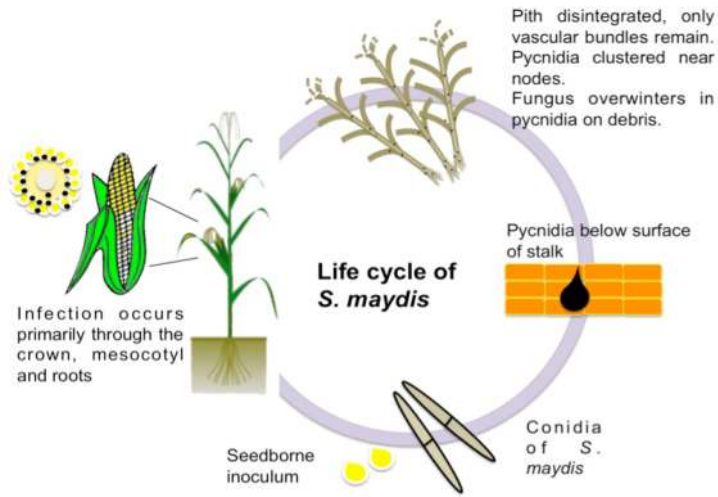


Figure 6. Life cycle of *S. maydis*. Pycnidia that contain the conidia are the principal dissemination source. A sexual stage for this ascomycete has not been described.

The incidence of infected maize by this phytopathogen in the field may range from 1 to 2% or as high as 75 to 80%. This fungus has a worldwide distribution but is mainly found in Guatemala, El Salvador, Belize, Brazil, South Africa, Australia, Asia, and the United States. In the United States this pathogen is the most important causing maize rot [45].

A sexual stage for this ascomycete has not been described. In the laboratory it can be maintained in solid media growing in filamentous form, when the growth is young, producing colonies which initially appear white, and then take on a green coloration with the production of metabolites (Figure 7). In submerged culture, the growth is in pellet form and on natural supports is in mycelial form [51].

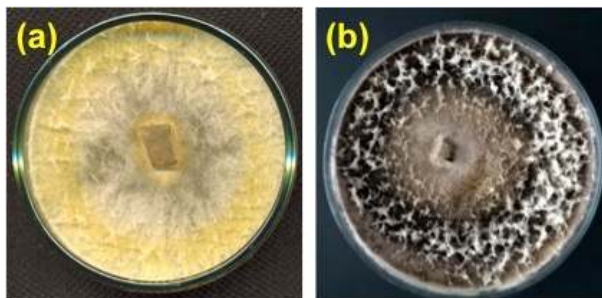


Figure 7. *S. maydis*, colonial morphology in Potato Dextrose Agar (PDA). After 7 days of growth the filamentous colony shows a white coloration (a), after 15 days of growth the filamentous colony shows a green coloration due to metabolite production (b).

S. maydis is also an important producer of mycotoxins among which are the diplodiatoxin, chaetoglobosins, and diplonine (Figure 8), all associated with a condition called diplodiosis, a mycotoxicosis characterized by neurological disorders such as ataxia, paralysis, and liver damage in farm animals fed infected corn. The same effect has also been observed in laboratory animals [41, 46–50].

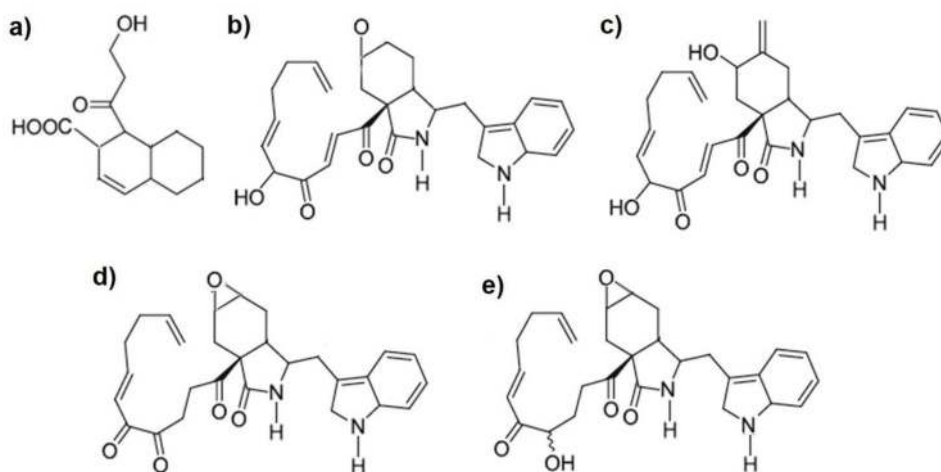


Figure 8. Structures of diplodiatoxin (a), chaetoglobosin K (b), chaetoglobosin L (c), chaetoglobosin M (d), chaetoglobosin O (e), diplonine.

2.2.2. Pathogenicity factors

Pathogenicity factors have not been described for this fungus; however, the effect of this ascomycete on the plant must be associated with the production of extracellular enzymes that macerate tissue allowing colonization, as already described for other fungi [26, 44].

S. maydis demonstrated the extracellular hydrolytic activities of acid protease, xylanases, and cellulases when it was grown on solid and liquid fermentation using a synthetic culture medium, as well as when the fungus was grown on the waste of crop maize (i.e., leaf, stem and broken corn), which functioned as inducers for the above mentioned enzymes, suggesting their possible role in the tissue degradation of the host [51].

2.2.3. Control of pathogen

Control of white rot on the stalk and corncob is made by agronomic practices and the use of resistant varieties; either method alter or interrupt the life cycle of the pathogen. There are resistant corn varieties on the market, however, the disease can develop in any hybrid if spore

levels are high and climatic conditions are found to favor infection. Proper crop rotation and elimination of infected crop residues can help to reduce the primary inoculum [42].

Another alternative treatment is the application of fungicides, however, the use of these compounds has been reduced due to their high toxicity. In this case, biological control has been an attractive option forming a component of a system of integrated management of disease, consequential to the decreased use of chemical compounds [38]. The biological control of *S. maydis* has been achieved experimentally, with different strains of actinomycetes demonstrating their potential to become tools for reducing disease [52, 53]. It has also been reported that strains of bacteria such as *Pseudomonas* spp., *Pseudomonas fluorescens*, *Pantoea agglomerans*, and *B. subtilis* inhibit the development of this fungus for the production of compounds with antifungal activity [54].

It is also important that in fields with significant levels of rot, corn must be harvested as soon as possible and dried below 15.5% moisture, to prevent contamination and mycotoxin production. The corn should be kept in installations that regularly allow grain aeration [43].

2.3. Biotechnological applications of *S. reilianum* and *S. maydis*

These phytopathogens have been considered of great importance due to the damage they cause crops; however, as they penetrate and colonize their hosts, enzymes which they produce should have attractive features for other applications. It has been determined that plant pathogenic fungi have a larger number of genes coding for these enzymes than fungi of industrial importance. The discovery of new enzymatic activities is very important for the development of efficient processes which depolymerize lignocellulosic materials used for obtaining bioproducts and biofuels [26].

S. reilianum secretes an aspartyl protease (Eap1) and a xylanase (SRXL1), which have already been purified and characterized biochemically. Eap1 has been shown to have the ability to degrade proteins in a corn plant and coagulate milk, suggesting it may have potential in the dairy industry, specifically in the production of cheese, or may be used to obtain protein hydrolysates of plant origin. Meanwhile, the xylanase SRXL1 presents interesting biochemical properties, having good stability over a wide range of temperature and pH. This suggests they could be used in the clarification of juices, increasing the performance and enhancing the maceration process, thus reducing the degree of viscosity. They may also improve the digestibility of straw destined as feed for ruminants [28, 29].

S. maydis is capable of producing hydrolytic enzymes such as cellulases, xylanases, and acid protease, into solid and liquid fermentation with different synthetic culture media, where it produces up to two isoforms of either xylanases or cellulases. When it was cultivated using biodegradable supports, it showed three isoforms of xylanases. The most interesting finding is that the fungus produced xylanolytic enzyme extracts free from cellulase activity [51]. These might be used in the paper industry facilitating the release of lignin from paper pulp, thereby reducing the use of chlorine as a bleaching agent, and avoid the degradation of cellulose.

Author details

Jorge Alvarez-Cervantes¹, Edna M. Hernandez-Dominguez², Maura Tellez-Tellez³, Virginia Mandujano-Gonzalez¹, Yuridia Mercado-Flores^{1*} and Gerardo Diaz-Godinez⁴

*Address all correspondence to: yuridia_utsh@hotmail.com; diazgd@hotmail.com

1 Polytechnic University of Pachuca, Hidalgo, Mexico

2 Higher Technological Institute of East of the State of Hidalgo, Hidalgo, México

3 Laboratory of Mycology, Biological Research Center, Autonomous University of the State of Morelos, Morelos, Mexico

4 Laboratory of Biotechnology, Research Center for Biological Sciences, Autonomous University of Tlaxcala, Tlaxcala, Mexico

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