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Article

Amaranth smut: biology, epidemiology and perspectives for sustainable management

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Abstract

Amaranth is a crop of great nutritional and social value in Mexico; however, its production is threatened by amaranth smut (*Thecaphora amaranthi*), a fungus that can cause losses of up to 100% in infected fields. This work gathers information on the pathogen until 2025 that can provide knowledge of the subject for new scientific studies. The pathogen forms resistant teliospores that remain viable in the soil for several years, making eradication difficult. There are no specific fungicides for its control; the suggested strategies for its control are the use of certified seeds, crop rotation and resistant genotypes. Understanding the interaction between the pathogen and its environment and host is essential for developing comprehensive programs that ensure the crop's sustainability and the producing communities' food security.

Keywords:

Thecaphora amaranthi, control, diagnosis.

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Introduction

Amaranth adapts to diverse climatic conditions, has nutritional, agronomic, industrial, and economic properties and is a great option for rural communities, generating investment and creating jobs in the countryside (Espitia *et al* ., 2010).

Amaranth is affected by pathogens that affect its development and production, such as amaranth smut (*Thecaphora amaranthi*), a fungus present in the seed that causes an aggressive, devastating disease capable of reducing grain yield by up to 100% (Espitia *et al*., 2010).

Smut fungi are a group of pathogens in the phylum Basidiomycota; they are distinguished by the formation of a resistant structure called a teliospore, which produces hyaline secondary spores; they are heteroecious, with a wide range of hosts. Phylogenetically, they belong to the class Ustilaginomycetes, the subclass Ustilaginomycetidae, the order Ustilaginales, the family Glomosporiaceae, and the genus *Thecaphora* (Smith *et al*., 2020).

Thecaphora is an important genus comprising about 65 species that infect hosts belonging to a wide variety of dicotyledonous families (Raza *et al*., 2022; Schuster *et al*., 2024). In recent years, its study has increased; nevertheless, several species of the genus have not been studied in depth (Díaz *et al*., 2024). The objective of the research was to comprehensively address the state of the art of *T. amaranthi* until 2025: biology, epidemiology, and management strategies, as well as advances in molecular diagnosis and sustainable control.

Biology of *Thecaphora spp.*

Thecaphora species have a single life cycle (Smith *et al*., 2020). They infect the plant, affecting its stigma and anthers during flowering. Once the fungus is established in the plant, generally before anthesis, it produces resistant reproductive structures called teliospores, which have thickened cell walls composed of residual material from the host's cell wall, and transform into galls, within which the fungus completes its life cycle, so it is not exposed to the environment, making the control of this pathogen extremely difficult (Arias *et al*., 2021).

The symptoms of smut are variable; the infection can range from a small spot or pustule to the complete transformation of the grains into a carbonaceous mass of teliospores. In some cases, hypertrophic pods have been observed without any internal signs of the pathogen (Bennett *et al*., 2021).

Pods severely affected by smut produce millions of teliospores inside. This characteristic is especially important during harvesting, since the pods can break during threshing, thereby dispersing the teliospores and contaminating the soil. In addition to this, teliospores survive for several years in the soil, preserving their viability without altering their infectivity (Cazón *et al*., 2016; Rago *et al*., 2017).

Thecaphora is a soil-dwelling fungus; the teliospores remain free and retain their capacity for infection for four years (Cazón *et al*., 2016). In some species, such as *T. frezii* , their longevity can reach up to six years, during which they can survive due to their latent metabolic state (Díaz *et al*., 2024). These characteristics of this pathosystem achieve the adaptation and permanence of smut in productive lots (Rago *et al*., 2017).

Thecaphora species

More than 90 *Thecaphora* hosts are known worldwide, some of which are of agricultural importance. Each species shows host specificity and they can vary in their geographical distribution and severity of the disease they cause (Vánky *et al*., 2008). Diseases caused by soil pathogens cause significant losses in various crops, often being destructive and of great economic importance (Katan, 2017).

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Amaranth smut (*Thecaphora amaranthi*) identified in amaranth plants; the main limitation in amaranth production is an aggressive and devastating disease that can reduce grain yield by up to 100% (Espitia *et al*., 2010).

Potato smut (*Thecaphora solani*) is one of the most important fungal diseases affecting potatoes, causing significant yield losses that often exceed 90% (Andrade *et al*., 2004). Peanut smut (*Thecaphora frezii*): most cultivars are susceptible to the pathogen, resulting in significant production losses of 35% (Marinelli *et al*., 2008).

Chinese rhubarb smut (*Thecaphora dahuangis*) accounts for 14% to 26% of yield losses in plantations in Gansu Province, China (Piatek *et al*., 2021), among others.

Distribution of *Thecaphora spp.*

Thecaphora species have a wide geographic distribution. They are found in the Americas, including Cuba, Argentina, Ecuador, and Mexico. They are also present in Australia, the Czech Republic, Germany, Romania, China, Finland, and Poland, depending on their host plants. This pathogen is transmitted by airborne teliospores, with wind being the most common means of dispersal of this smut (Bernal *et al*., 2000; Pérez *et al*., 2002; Piatek *et al*., 2021).

Incidence factors of *Thecaphora spp.*

Some studies showed a significant linear relationship between estimated yield losses and disease intensity, and that a lower soil water content of 30% significantly predisposes to greater smut infection (Paredes *et al*., 2017).

The increase in the disease's prevalence indicates that contaminated seed has been the primary vehicle of introduction into the different producing regions (Cazón *et al* ., 2016).

The optimal thermal range for the pathogen's development is 16-27 °C; 25 °C was found to be optimal for teliospore germination. For its development, the pathogen requires high relative humidity, close to 100%, maintained for prolonged periods without significant decreases.

As the aboveground part shows no symptoms, the fungus went unnoticed for many years by technicians and producers. Smutted pods produce millions of teliospores that gradually increase the inoculum in the soil. This increased the disease pressure observed year after year (Espitia *et al*., 2010).

Agricultural machinery and crop seeds can be contaminated by *Thecaphora* spores and can also contribute to the spread of the pathogen, as is the case with various soil pathogens (Katan, 2017).

Given the size of the teliospores, affected pods can break during pulling and threshing operations, releasing large quantities of spores that, together with soil and dust, can be carried by air currents up to at least 40 meters away and deposited in surrounding lots. The constant increase in disease intensity is largely due to increased inoculum in soils, which is further enhanced by the disease's aggressiveness and the number of teliospores produced by smut infections (Paredes *et al*., 2021).

Thecaphora amaranthi

In 1945, Hirschhorn identified the smut that attacks amaranth species (*Glomosporium amaranthi*). In 1994, Vánky reclassified *Glomosporium amaranthi* Hirsch, transferring it to the genus *Thecaphora* , resulting in the proposed new combination *Thecaphora amaranthi* (Hirschhorn). It is present in several Amaranthaceae species: *Amaranthus* hybridus, A. quitensis, A. retroflexus, and A. spinosus (Pérez *et al*., 2002).

In their study, Bernal *et al*. (2000) identified amaranth smut in samples collected in San Miguel del Milagro, Tlaxcala, Mexico. They reported that it attacks the inflorescences and develops at the expense of the ovary, forming dark cinnamon, globose sori (Figure 1).

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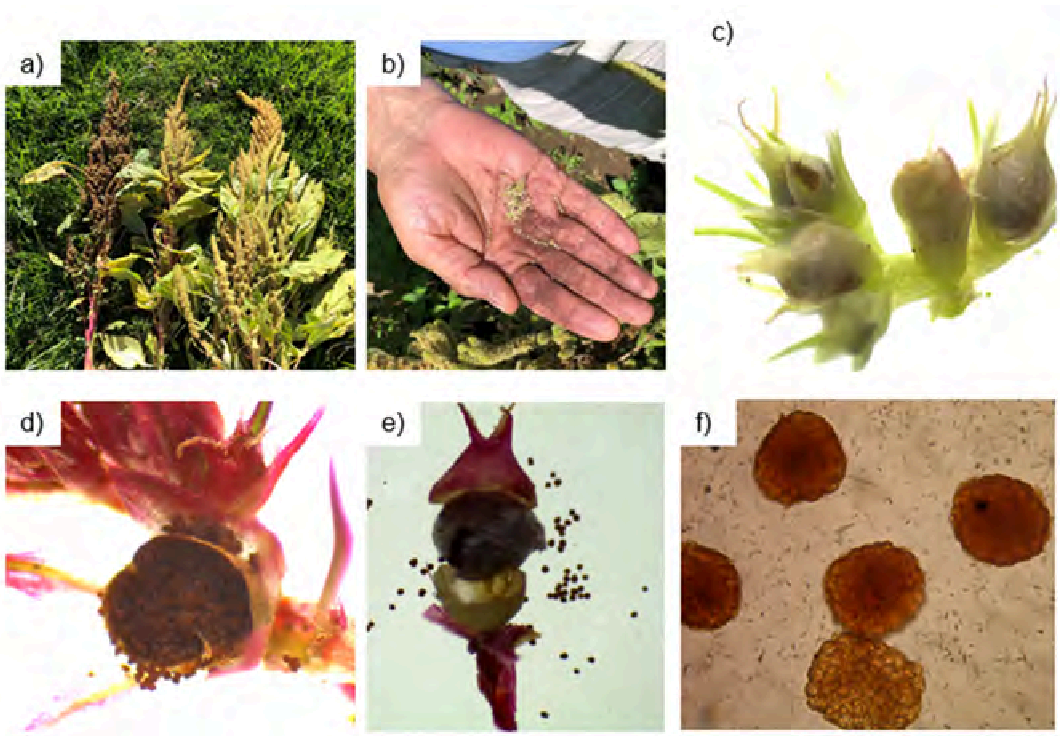
Figure 1. Different aspects of *T. amaranthi* : a) plant infected by amaranth smut; b) a mass of teliospores detached upon contact with the panicle; c) inflorescences forming dark cinnamon, globose sori; d) pyxidium with teliospores; e) transformation of grains into teliospores; and f) mature teliospores.



Amaranth smut is a monocyclic disease, meaning it causes only one infection in the susceptible organ during the cultivation cycle; it does not produce secondary inoculum that reinfects the host within the same generation. It is a polyetic disease; spores accumulate in soils year after year, triggering higher concentrations of inoculum (Rago *et al* ., 2017).

Not all ovaries are attacked by the fungus. Those that are not used for sorus development produce seemingly normal seeds. As with any monocyclic disease, the amount of initial inoculum is one of the parameters that best explain the epidemic (March *et al* ., 2010). In this sense, the incidence of the disease will depend mainly on the number of teliospores present in the soil at the time of crop planting (Conforto *et al* , 2019).

It is a biotrophic pathogen (Arias *et al*., 2021); it mainly attacks plants with poor development. Because the area where amaranth is grown is a continuous monoculture, a substantial increase in the inoculum was observed in both the seed and the soil. Amaranth smut is considered the main disease limiting production (Espitia *et al* ., 2010).

Ecology and epidemiology of *T. amaranthi*

The incidence of amaranth smut is closely linked to the soil and climatic conditions of the production system. *T. amaranthi* teliospores can remain viable in the soil for more than four years, with germination capacity at temperatures between 16 and 27 °C and a relative humidity close to 100% (Cazón *et al*., 2016; Rago *et al*., 2017).

It has been observed that soils with low water availability and continuous *Amaranthus* monocultures promote an increase in inoculum and the pathogen's persistence (Paredes *et al*., 2017).

In addition, the soil microbiota plays a modulating role in infection dynamics. Antagonist fungi such as *Trichoderma spp.* and rhizospheric bacteria of the genus *Bacillus* can reduce teliospore viability through competition or antibiosis, suggesting potential for integrated biological management (Matas et al., 2023 .

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Life cycle of *T. amaranthi*

The infection occurs when the plant penetrates the soil, releasing exudates that stimulate the germination of teliospores present in the soil, thereby generating a local infection (Marinelli *et al*., 2008). At germination, the teliospore (diploid) produces a germ tube, into which the nucleus migrates, forming a promycelium or probasidium.

The nucleus then divides by meiosis to form haploid cells, developing the basidiospores (haploids). The basidiospores germinate to produce haploid hyphae, which conjugate with others of different polarity (somatogamy); the dikaryotic state is restored, and an infective dikaryotic hypha is produced. This hypha penetrates the plant, infecting the fertilized ovary and thereby initiating infection (Arias *et al*., 2021).

Teliospores wait until the plant develops structures that penetrate the soil to germinate, infect, and colonize the host. A key characteristic is that the plant shows no visible symptoms in the aboveground part, and the pathogen does not translocate to any other organ of the plant; it produces the disease in the same organ that it infects, colonizes, and sporulates (Marinelli *et al*., 2008).

The infection produced in the ovary will accompany the fruit's development, and the symptom will be observed at harvest, when the plant will leave the teliospores exposed when uprooted, and they will disperse to complete their cycle.

Diagnosis and molecular detection

The diagnosis of *Thecaphora amaranthi* has evolved from classical morphological identification to high-precision molecular methods. Analysis of ribosomal regions using the universal primers ITS1/ITS4 and some specific primers [TF2F (5'ATGTCAAAGAGTGCGAAGAC3') and TF2R (5'TATCTTGCTGGTAGGCTGTT3')] has been shown to be effective in distinguishing species of the genus *Thecaphora* , including those with similar morphology such as *T. frezii* and T. solani (Cazón *et al*., 2016).

PCR amplification with specific primers enables the detection of traces of fungal DNA in seeds, soils or plant material, thereby facilitating both phytosanitary certification and the prevention of dissemination (Cazón *et al*., 2016).

Recently, qPCR and Loop-Mediated Isothermal Amplification (LAMP) tools have been developed to quantify the inoculum load in soil, and these methods have helped establish a relationship between spore density and disease severity in plants (Pacheco *et al*., 2025).

The design and evaluation of LAMP primers focus on the specific detection of pathogens in the soil; the successful implementation of this assay as a portable device would provide farmers and agronomists with a valuable tool for early and accurate pathogen diagnosis, thereby allowing timely disease management interventions (Pacheco *et al*., 2025).

Management and control strategies for *Thecaphora*

Given the absence of registered fungicides with proven efficacy against *Thecaphora amaranthi* , management strategies should focus on preventive measures and sustainable agroecological practices. The primary prevention of *Thecaphora* infection and the spread of the pathogen begin with the producer, who uses tools that, if not disinfected, disseminate spores.

The use of resistant cultivars is a viable and sustainable means of controlling the pathogen (Valente *et al*., 2023). Effective disease management strategies are agricultural practices, such as stubble removal, crop rotation with non-host species, use of pathogen-free seed, and disinfection of machinery (Figure 2).

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Figure 2. Effective management strategies for *T. amaranthi* : a) review the plot; b) identify plants affected by the fungus; c) eliminate them; and d) bury them.

Socioeconomic impact

Amaranth smut poses a serious threat to food production and security in rural regions of Mexico and Latin America. Losses of more than 80% in severely infested lots directly affect the economy of small producers and compromise the availability of high-nutritional-value food (Espitia *et al*., 2010).

Despite its importance, limited knowledge of its biology, epidemiology, and control limits the formulation of effective phytosanitary policies. The implementation of monitoring and producer training programs is essential to reduce the spread of the pathogen and ensure the sustainability of the crop.

Conclusions

Thecaphora amaranthi is a pathogen of increasing relevance to amaranth cultivation in Mexico and regions of the Americas. Its capacity for prolonged persistence in the soil, the difficulty of its early detection and the absence of chemical control demand a comprehensive approach in prevention, ecological management and the implementation of biotechnology as an innovative and precise tool.

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It is necessary to strengthen research on molecular diagnostics, genetic variability and host resistance, and to evaluate the influence of the soil microbiome on the pathogen's dynamics. Understanding the mechanisms of infection and survival of *T. amaranthi* will enable the establishment of sustainable management strategies that protect both agricultural productivity and the nutritional and cultural value of amaranth.

The development of inter-institutional programs that integrate science, innovation, and agricultural extension will be key to mitigating the impact of smut and ensuring food security in amaranth-producing communities.

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