Tar spot: an understudied disease threatening corn production in the Americas

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Abstract

Tar spot of corn has been a major foliar disease in several Latin American countries since 1904. In 2015, tar spot was first documented in the United States and has led to yield losses of approximately 4.5 million t annually. Tar spot is caused by an obligate pathogen, *Phyllachora maydis,* and thus requires a living host to grow and reproduce. Due to its obligate nature, biological and epidemiological studies are limited and impact of disease in corn production has been understudied. Here we present the current literature and gaps in knowledge of tar spot of corn in the Americas, its etiology, distribution, impact and management strategies as a resource for understanding the pathosystem. This review is intended to guide current and future research and aid in the development of more effective management strategies for this disease.

Introduction

Tar spot caused by *Phyllachora maydis* Maubl*,* an obligate fungus, is a major foliar disease of corn. Tar spot can reduce grain yield, and quality of silage, stover, and husks (Maublanc 1904; Hock et al. 1989; Bajet et al. 1994). In Latin America, economic damage of up to 50 percent has been documented when epidemics are severe early in the crop's reproductive phases. *P. maydis* is endemic to Latin America, where it was first identified in Mexico in 1904 (Maublanc 1904; Abbott 1931; Malaguti and Subero 1972; Liu 1973; Bajet et al. 1994). Beginning in 2015, *P.*

maydis appeared and has spread in the Midwestern United States (Bissionnette 2015; Ruhl et al. 2016; McCoy et al. 2018; Dana Lana et al. 2019; Malvick 2020).

In Latin America, tar spot is purportedly associated with two additional fungi(Hock et al. 1995): *Monographella maydis* Müller & Samuels, a necrophyte, and *Coniothyrium phyllachorae* Maubl, a fungal hyperparasite (Hock et al. 1995). In the U.S., however, only *P. maydis* has been documented in association with tar spot (McCoy et al. 2019). The disease can cause corn grain yield losses ranging from 11 to 46 percent in Latin America (Hock et al. 1989; Pereyda-Hernández et al. 2009). Corn grain yield losses of up to 25 to 30 percent were recently reported in the Midwestern U.S. (Telenko et al. 2019; Mueller et al. 2019). Due to a lack of information about this pathosystem and the dire threat tar spot poses to U.S. corn production, there is a pressing need for research on the biology, ecology, epidemiology, and management of the organism(s) that cause tar spot. This Feature Article reviews the available literature on tar spot of corn and the other species associated with this disease to help guide current and future research on this economically important pathosystem.

Signs, symptoms, causal agent(s), and host range

Tar spot is characterized by the formation of black stromata, the fruiting bodies of *P. maydis*, on the foliage. The stromata resemble spots of tar (Fig. 1). Like other species in the genus, *P. maydis* is an obligate biotroph, requiring a living host to grow and reproduce (Cannon 1991). In fields with infested corn residue, initial signs and symptoms of tar spot may appear in the lower canopy of the corn plant (Bajet et al. 1994). In the U.S., however, “top down” patterns of symptom development, in which upper portions of the plants exhibit symptoms first, occur

frequently in sites where new outbreaks occur, suggesting long distance transmission of inoculum. For instance, plants of any age, leaves, leaf sheaths, and husks are susceptible to infection (Bajet et al. 1994; Hock et al. 1995).

Infection by *P. maydis* results in the development of glossy structures (masses of black fungal tissue) known as stromata (Fig. 2) (Hock et al. 1995; Carson 1999; CIMMYT 2003). Stromata are embedded in host tissue and scattered across or clustered on both leaf surfaces, occasionally coalescing into stripes (Liu 1973). Stromata are sometimes enclosed by brown, elliptical, necrotic halos referred to as "fisheye lesions" (Fig. 3). In severe cases, necrotic halos coalesce, causing extensive necrosis and leaf blight leading to premature senescence and death of plants (Ceballos and Deutsch 1992; Hock et al. 1995; Carson 1999). The host range for *P. maydis* appears to be restricted to *Zea mays* (Cline 2005), although other *Phyllachora* species cause tar spot on a wide range of grass species and other hosts (Parbery 1967, 1971).

Older literature indicated that fisheye lesions were always associated with the presence of the fungus *Monographella maydis* (Muller and Samuels 1984; Ceballos and Deutsch 1992; Hock et al. 1992; Bajet et al. 1994; Hock et al. 1995). However, these results were based on limited surveys, identification was based solely on morphological characteristics, and no voucher specimens were deposited. In Latin America, infection by *P. maydis* or *M. maydis* alone was initially considered to be of minor importance (Müller & Samuels 1984; Hock et al. 1991). Dual infection with *M. maydis* and *P. maydis* was implicated in significant leaf necrosis and yield loss (CIMMYT 2003). In field conditions where both fungi were present, researchers speculated that *M. maydis* entered plants following infection by *P. maydis* and subsequently produced a toxin that caused the fisheye lesions. However, in Mexico,

Ecuador, Honduras, and the U.S., fisheye symptoms were sometimes present but *M. maydis* was absent (Ceballos and Deutsch 1992; Ruhl et al. 2016; McCoy et al. 2019). McCoy et al. (2019) carried out a Next-Generation sequencing analysis to determine if *M. maydis* was present in fisheye lesions on samples collected in Michigan, and to identify the different fungi found in tar spot lesions with and without fisheye symptoms. Two *Microdochium* spp. operational taxonomic units (OTU) were identified; however, neither was abundant nor associated consistently with fisheye symptoms. No evidence of *M. maydis* was found among U.S.-associated fisheye samples (McCoy et al. 2019).

Another fungus, *Coniothyrium phyllachorae* Maubl was also speculated to be associated with stroma of *P. maydis* (Maublanc 1904; Müller & Samuels 1984). *C. phyllachorae* is a fungal hyperparasite that destroys perithecia produced by *P. maydis* (Maublanc 1904), suggesting that *C. phyllachorae* may be used as a biological control for tar spot rather than being responsible for tar spot symptoms. However, this potential management strategy has not been tested (Hock et al. 1995). The observation that tar spot lesions containing *C. phyllachorae* are usually smaller than lesions containing *M. maydis* (Hock et al. 1989, 1995) has not been explained.

Biology of spores

P. maydis is an ascomycete, producing sexual spores (ascospores) and asexual spores (conidia) (Figs. 4 and 5). Ascospores are formed in single-walled asci within a single perithecium covered by stromata. Eight oval to ovoid ascospores, 10-14 µm by 5.5-8 µm, are produced per ascus (Maublanc 1904; Liu 1973; Hock et al. 1992). Ascospores are discharged through the perithecial ostiole in a

mucilaginous mass (Fig. 6). A single perithecium will discharge spores repeatedly over the course of several days, occasionally producing pale cirrhi (Parbery 1963). Ascospores require a temperature range of 20 to 25°C for optimal germination with relative humidity >75% and prolonged periods of leaf wetness (Maublanc 1904; Hock et al. 1989; Bajet et al. 1994; Pereyda-Hernández et al. 2009; Groves et al. 2020). Dittrich et al. (1991) found that in laboratory studies ascospore germination can occur in as little as 2 h in distilled water at 24°C. These researchers also indicated that ascospore germination and formation of appressoria by *P. maydis* occurred between 10 and 20 °C, with appressoria forming within 12 to 24 h, which is consistent with other members of the genus (Parbery 1963).

Phyllachora maydis can overwinter on plant residue. In Mexico, on infected corn material that was left uncovered on the soil surface for 3 months, ascospores had a maximum germination rate of 3%. Recent studies by Kleczewski et al. (2019) and Groves et al. (2020) showed that ascospores overwintered in the Midwestern U.S. on corn residue despite harsh winter weather conditions (a low of -34°C air temperature); these ascospores were able to germinate and infect seedlings under controlled conditions. Nevertheless, neither the mechanisms of overwintering nor the existence of alternative plant hosts of *P. maydis* is known (Mottaleb et al. 2019, Groves et al. 2020).

The pycnidial stage of *P. maydis* (*Linochora maydis*) may also be present in the form of filiform spermatia. Spermatia are 10-15 µm by 0.5 µm and are produced in pycnidial fruiting bodies, which are often found with perithecia in stromata. According to Parbery (1967) and Muller and Samuels (1984), these spores may fulfill the role of conidia in the *Phyllachora* life cycle.

The genus *Microdochium* spp. includes important plant pathogens, particularly on grasses and small grain cereals (Von Arx 1987). *Microdochium* spp. are recognized as *Fusarium*-like fungi due to similar spore morphology. However, the conidiogenous cells in *Microdochium* spp. are not phialidic as in true *Fusarium* species and the conidia have a truncate base rather than 'foot-cells' (Von Arx 1987). *Monographella maydis* (Syn. *Microdochium maydis* E. Müll. & Samuels) was first described in 1984 from leaf tissue in Mexico (Muller and Samuels 1984; Von Arx 1987; Hock et al. 1992; Bajet et al. 1994). Both the teleomorph and anamorph of *M. maydis* were recovered from fisheye lesions, and inoculation of corn plants naturally infected with *P. maydis* and *M. maydis* conidial suspensions caused the characteristic fisheye lesions and significantly increased disease severity (Hock et al. 1992). However, a lack of methodological details in the Hock et al. (1992) study limits the credibility of these observations.

Monographella maydis forms single-walled asci within perithecia immersed in host tissue, eventually erupting through the epidermis. Eight fusiform ascospores, 18 to- 22 µm by 3.5 to 5 µm and containing 1 to 3 transverse septa, are produced per ascus. Conidia produced in sporodochia are hyaline, elongate, mostly curved, 20-46 µm by 3-4 µm with 3-9 transverse septa. The sexual stage of the pathogen is rarely found in the field. Conidial germination was greatest at 25°C in darkness (Dittrich et al. 1991). In inoculation trials during this research, infection of corn with *Monographella maydis* by itself was achieved in only one of eight attempts under 38/18°C day/night temperatures and 80-100% relative humidity. *Monographella maydis* persists on infected crop residue, with conidia remaining viable for 109 days on detached leaves at room temperature (Hock et al. 1992).

Disease cycle

The disease cycle of tar spot is not fully understood. However, ascospores and conidia of *P. maydis* can overwinter in stromata on decaying corn leaves or residue in fields (Kleczewski et al. 2019; Groves et al. 2020). Hence, infested residue with propagules are likely the source of primary inoculum. According to Hock et al. (1992), ascospores are released from stromata and disperse either by wind or rain splash to foliage during periods of moderate temperature (16 to 23°C), leaf wetness duration of greater than 7 hours per night, and relative humidity >75% (Hock et al. 1995). Long-distance spore dispersal is another possible source of primary inoculum. However, ascospore dispersal has been documented to only as far as 31 m from the source of the inoculum (Liu 1973). Ascospores infect nearby corn plants and this cycle will repeat multiple times per growing season under conducive conditions (Hock et al. 1989; Bajet et al. 1994). In the U.S., in fields with no previous history of the disease, tar spot symptoms appeared first in the upper crop canopy (Robertson, A. 2019, Malvick, D. 2020 - personal communication). These observations raise questions about the possibility of long-distance dispersal. Neither the incubation period (time from inoculation to symptom development) nor latent period (time from inoculation to onset of reproductive structures) (Parlevliet 1979) has been clearly established for *P. maydis*. Preliminary data from two of our labs indicated that the latent period can be variable, between 14 nd 20 days at 16 to 23°C (Cruz and Kleczewski unpublished data). The duration of latent periods can be strongly influenced by growing degree days (GDD) and host resistance level (Precigout 2020).. Symptoms of tar spot are observed 14 days after infection and new ascospores are produced in stromata soon thereafter (Hock et al. 1995). A

schematic representation of the presumed disease cycle of tar spot in the U.S. is shown in Figure 7.

Geographical Distribution

P. maydis is endemic to parts of Mexico as well as Central and South America (Fig. 8, Table 1), where it was apparently restricted for >100 years (Hock et al. 1995; Cline 2005). However, in 2015 it was detected for the first time in the U.S. and has spread significantly in the U.S. since then (Bissonnette 2015; Ruhl et al. 2016). In the U.S., *P. maydis* is now established in the states of Illinois, Indiana, Iowa, Michigan, Minnesota, Missouri, Ohio, Wisconsin and Florida (Fig. 8) (Bissonnette 2015; Ruhl et al. 2016; McCoy et al. 2018; Dalla Lana et al. 2019; Malvick et al. 2020). Multiple pathways have been proposed for the introduction of *P. maydis* into the U.S. (Ruhl et al. 2016; Mottaleb et al. 2019). Although *P. maydis* is not known to be seedborne, imported grains contaminated with leaf/husk residue can be a source of inoculum (Richardson, 1990).

Molecular diagnostics

The biotrophic nature of *P. maydis* makes it difficult to study in the laboratory, as it has never been cultured on synthetic medium (Muller & Samuels, 1984). The use of genetic technologies such as DNA diagnostics (amplification and sequencing) can compensate for this difficulty and provide a better understanding of the fungus. Prior to 2015, no *Phyllachora* spp. genomes had been sequenced, and hence no comparative sequence data were available in GenBank, NIH genetic sequence database, or the U.S. National Fungus Collection (BPI) (Ruhl et al. 2016). *Phyllachora* spp. were diagnosed mainly via symptom and morphological characters

(Maublanc 1904; Parbery 1963; Muller & Samuels 1984; Hock et al. 1995; Ruhl et al. 2016). However, due to the recent documentation of *P. maydis* in the U.S., molecular diagnostic data are now available in GenBank and the NIH genetic sequence database. DNA was extracted from stromata that had been aseptically removed from corn leaves collected in each of the affected U.S. states, sequenced, and deposited in the U.S. National Fungus Collections (BPI) (McCoy et al. 2018). Currently, sequences for the internal transcribed spacer (ITS) regions of the ribosomal RNA gene are the only genetic sequences available for *P. maydis* in GenBank (Ruhl et al. 2016; McCoy et al. 2018). There are 67 specimen records for *Phyllachora maydis* and its synonyms in the U.S. National Fungus Collection (BPI), of which only five specimens were deposited based on molecular identification via ITS sequence confirmation. The current ITS sequences reported in the GenBank for identification of *P. maydis* are listed in Table 2.

A draft genome sequence of *P. maydis* (Telenko et al. 2020) was recently published which will provide an important resource for further studies on the origin of *P. maydis* in the U.S., population structure, genetic diversity and phylogenetic relationships among *Phyllachora* spp.

In a recent paper, phylogenetic relationships among species in the order Phyllachorales were inferred based on Bayesian analysis incorporating sequence information from five molecular characters: 1) nuclear large subunit ribosomal DNA (nrLSU rDNA); 2) nuclear small subunit ribosomal DNA (nrSSU rDNA); 3) internal transcribed spacer ribosomal DNA (ITS rDNA), and the protein coding genes; 4) DNA-directed RNA polymerase II subunit 2 (RPB2); and 5) Elongation factor 1-alpha (TEF1) (Mardones et al. 2017). It is interesting to note that *P. maydis* showed close

similarity to other *Phyllachora* spp. for all five of the molecular regions considered but appeared to be most closely related to *P. graminis* (Mardones et al. 2017).

A study by Hernández-Restrepo et al. (2016) used ITS, Elongation factor 1 alpha (EF1α), RNA polymerase II second largest subunit (RPB2), and small subunit nuclear ribosomal DNA (nrSSU) regions to construct a phylogenetic tree of the Phyllachorales, validating the use of these regions and generating sequences that could be adapted for future work with *P. maydis.* To date, there are three phylogenetic trees published with similar loci, but for the *Phyllachora* portion only the ITS gene was used, and species distinctions within the genus still need to be resolved.

A recent re-evaluation of *Monographella* considered four loci for use in taxonomic and phylogenetic studies of this genus. Of the four, the partial beta-tubulin gene region was found to be the most informative, with the RNA polymerase II second largest subunit gene (RPB2) also recommended. The translation elongation factor 1 alpha gene has also been used to differentiate between *Monographella* spp. Unfortunately, no genetic data for *M. maydis* exists in public databases (Hernández-Restrepo et al. 2016).

Genetic basis of host resistance and breeding for resistance

Deploying host resistance is potentially both an economical and effective means of managing tar spot. A range of reactions to *P. maydis* have been observed in diverse corn germplasm, indicating that a range of resistance to tar spot exists (Ceballos and Deutsch 1992; Mahuku et al. 2016; Cao et al. 2017). Furthermore, the heritability of tar spot resistance is moderate to high, indicating that breeding to develop resistant populations is possible (Cao et al. 2017).

The genetic architecture of tar spot resistance is complex, but a single large-effect locus for resistance has been consistently detected (Ceballos and Deutsch 1992; Mahuku et al. 2016; Cao et al. 2017). An early study utilizing three segregating bi-parental populations found resistance to symptoms caused by *P. maydis* to be highly heritable and dominant in nature (Ceballos and Deutsch 1992). More recently, a large-effect quantitative trait locus (QTL) located in chromosomal bin 8.03, referred to as *qRtsc8-1*, was consistently detected across multiple tropical/subtropical populations of corn screened in several locations across Central and South America (Mahuku et al. 2016; Cao et al. 2017). When detected, *qRtsc8-1* accounted for 18-43% of the observed phenotypic variation in disease severity (Mahuku et al. 2016; Cao et al. 2017). It is interesting to note that the most significant association identified by Mahuku et al. (2016) in a genome-wide association mapping study was with a leucine-rich repeat receptor-like encoding gene, which would be consistent with a major resistance gene. Several haplotypes were identified in *qRtsc8-1* that increased resistance (Mahuku et al. 2016). Together, these results indicate that marker-assisted selection for resistant *qRtsc8-1* haplotypes might be an effective strategy for developing tar spot resistant varieties.

Hybrid reaction and susceptibility to tar spot

A study by Telenko et al. (2019) evaluated corn hybrid reactions to tar spot during the 2018 U.S. Midwest epidemic. In that study, all hybrids rated were susceptible to tar spot pathogen. Severity of leaf symptoms ranged from minor (1-15%) to severe (40-50%). Data from these hybrid trials demonstrated a range in hybrid susceptibility and reaction to tar spot, where every 1% increase in tar spot severity resulted in an estimated 21.5 to 91.5 kg/ha loss (Telenko et al. 2019).

Future outlook and challenges

Tar spot has become a high-profile emerging disease in the U.S. due to its recent identification and spread, documented impact on corn yields, and the threat it poses to corn production. Mottaleb et al. (2019), indicated that tar spot can become established throughout the U.S. Corn Belt. Unfortunately, there is a general lack of information about this pathosystem.

For instance, currently there is no evidence of *M. maydis* association with fisheye lesions in the U.S. Hence, future research that surveys a large collection of tar spot-infected corn from different regions would help test previously established hypotheses and provide critical information to understand this disease and fisheye symptom development. Hypotheses that may explain these observations are that fisheye lesions are a result of *P. maydis* infection alone, and/or specific pathogen x host x environmental conditions result in their development. Alternatively, fisheye lesions may be caused by a different fungus that was incorrectly identified as *M. maydis* in previous studies. This hypothesis is difficult to confirm as no vouchers of *M. maydis* exist from the initial species description and no molecular data exist for *M. maydis* (Hernández-Restrepo et al. 2016). *Monographella* previously were defined as members of the genus *Fusarium.* Could certain local species of *Fusarium* be responsible for fisheye development? Finally, an unidentified organism may be the cause for the development of fisheyes.

The events underlying *P. maydis* emergence in the U.S. are currently unknown. Thus, there is need for investigating the genetic diversity and population structure of *P. maydis.* This information will help determine whether *P. maydis* was an endemic pathogen already present in the U.S. that underwent genetic changes

that resulted in the ability to infect corn, or whether *P. maydis* was introduced to the U.S. by movement of people, crop material, or weather systems.

Developing effective and long-lasting prevention strategies is key for tar spot management. For that reason, we need to increase the current understanding of pathogen biology and disease epidemiology, which would include a better understanding of changes in disease intensity over time and space. Visual tar spot surveillance methods and diagrammatic scales that partition severity into predetermined stroma or fisheye/necrotic severity classes are available (Hernández and Islas 2015). However, these diagrammatic scales are based on leaf sections rather than the whole leaf; this might present a challenge as symptoms might not be uniform across the leaf blade. Although the development and diversity of tar spot symptoms has not been characterized thoroughly, such work is foundational for disease phenotyping. The information generated is key to developing epidemiological criteria to support breeding tactics (Fernandez-Campos and Gongora-Canul et al. 2020) against this disease. Autonomous aerial vehicles offer an alternative for tar spot phenotyping since they can be equipped with a range of sensors that measure spectral reflectance (Loladze et al. 2019; Mahlein et al. 2016). Several vegetation indices obtained from multispectral and thermal data have been correlated with tar spot severity and losses of grain yield in the absence of fungicide treatment (Loladze et al. 2019). Future studies in this area should determine whether remote sensing platforms are capable of describing temporal and spatial dynamics of the disease (Gongora-Canul et al. 2020).

Effective management strategies for tar spot are limited and are based on what is known of tar spot in Mexico, Central America, and South America (Kleczewski et al. 2019). Limited field data is available from the U.S. Kleczewski et

al. (2019) proposed that management strategies need to target environmental conditions, fungal populations, hybrid genetics and cropping systems associated with each region. Tar spot management strategies have been recommended but remain limited in the U.S. due to the recent appearance of this pathogen. These strategies include (1) avoid highly susceptible hybrids, (2) consider applicaton of fungicides with mixed mode of action at appropriate timing close to the onset of the epidemic, (3) manage irrigation, (4) rotate crops to allow *P. maydis* infected residue to decompose, and (5) remove residue from fields (Kleczewski et al. 2019; Telenko et al. 2019). Though fungicides are available for managing tar spot, the optimum timing and number of applications needed if an early epidemic occurs is not well established. Teams are also working on the development of a reliable protocol for artificial inoculations under controlled environments, and to determine economically sound management options for combatting tar spot.

Host resistance will become an important tool for control of tar spot. Little is known about resistance in germplasm adapted to the U.S. and whether previously identified QTLs will be effective against *P. maydis* populations in the U.S. Furthermore, genomic selection is a powerful tool that can take advantage of many small-effect loci to develop resistant lines (Meuwissen et al. 2001; Poland and Rutkowski 2016). Genomic prediction models had moderate-to-high prediction accuracy for tar spot, showing promise that genomic selection may be an effective method to improve tar spot resistance in breeding programs (Cao et al. 2017).

We believe that the development of effective management strategies for this understudied pathogen requires increased understanding of its biology and epidemiology, and developing and deploying rapid diagnostic methods, effective

368 weather-based warning systems, systematic surveillance, and resistant germplasm
369 for regions at risk.
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550 **Table 1: Geographical Distribution of tar spot based on available reports.**

Continent/Country	Year documented	Source
Central, South America and Caribbean		
Peru	1931	Abbott (1931)
Dominican Republic, Guatemala	1944	Orton (1944); Bajet et al. (1994)
Bolivia	1949	Stevenson and Cárdenas (1949); Bajet et al. (1994)
Trinidad and Tobago	1951	Baker and Dale (1951)
U.S. Virgin Islands	1951	Stevenson (1975)
Honduras, Nicaragua, Panama	1967	McGuire and Crandall (1967)
Cuba	1968	Arnold (1986)
Colombia	1969	Castaño (1969); Bajet et al. (1994)
Venezuela	1972	Malaguti and Subero (1972); Bajet et al. (1994)
Puerto Rico	1973	Liu (1973); Bajet et al. (1994)
El Salvador, Haiti, Ecuador, Costa Rica,	1994	Bajet et al. (1994)
North America		
Mexico	1904	Maublanc (1904); Hock et al. (1989)
U.S. (Indiana and Illinois)	2015	Bissonnette (2015); Ruhl et al. (2016)
U.S. (Florida, Iowa, Michigan, Wisconsin)	2016	McCoy et al. (2018)
U.S. (Ohio)	2018	Dalla Lana et al. (2019)
U.S. (Minnesota, Missouri)	2019	Bissonnette (2019) - personal communication; Malvick (2020)

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553 **Table 2: GenBank's available sequences for *P. maydis* identification.**

Collection location	(NCBI Voucher) GenBank ID	Source
Indiana	(BPI 893231) No. KU184459	Ruhl et al. (2016)
Iowa	(BPI 910561) No. MG881848.1	McCoy et al. (2018)
Michigan	(BPI 910562) No. MG881847.1	McCoy et al. (2018)
Ohio	(18AP065) No. MK184990	Dalla Lana et al. (2019)
Wisconsin	(BPI 910560) No. MG881846	McCoy et al. (2018)

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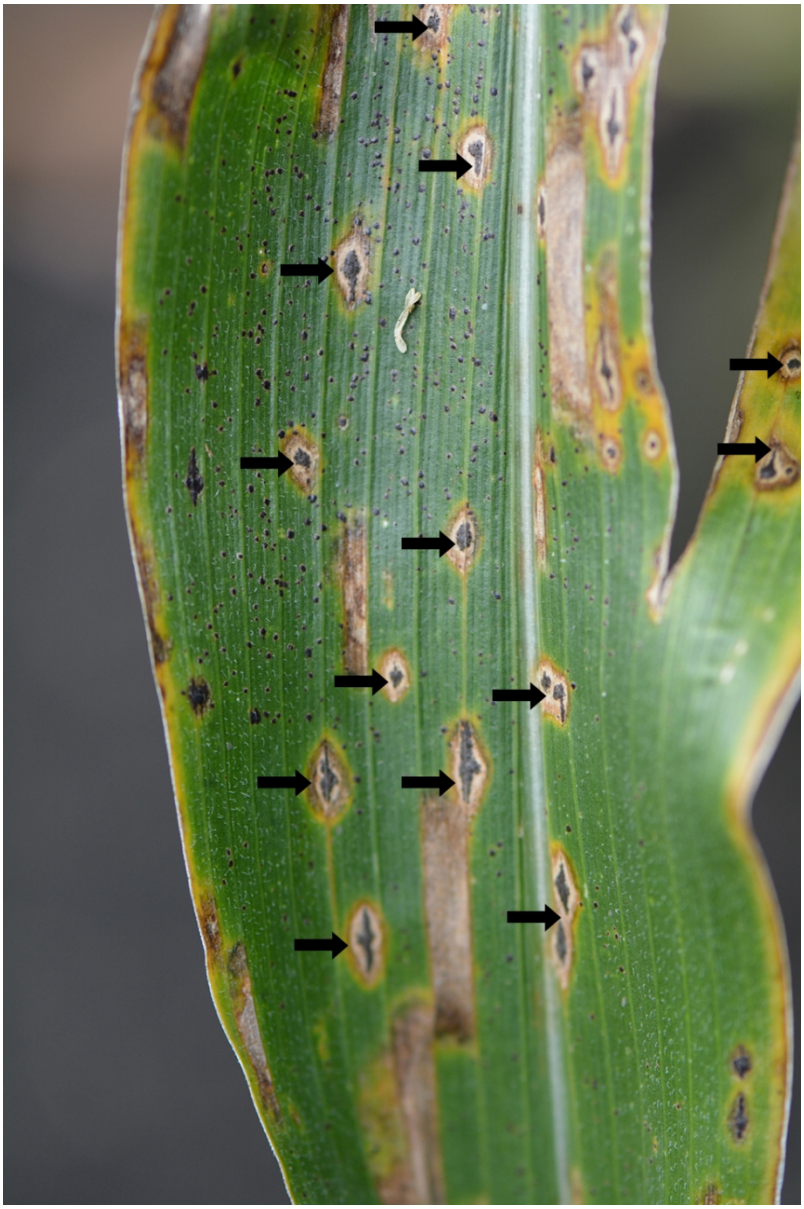
Fungal fruiting bodies of *Phyllachora maydis* on the foliage resemble spots of tar.

82x205mm (300 x 300 DPI)

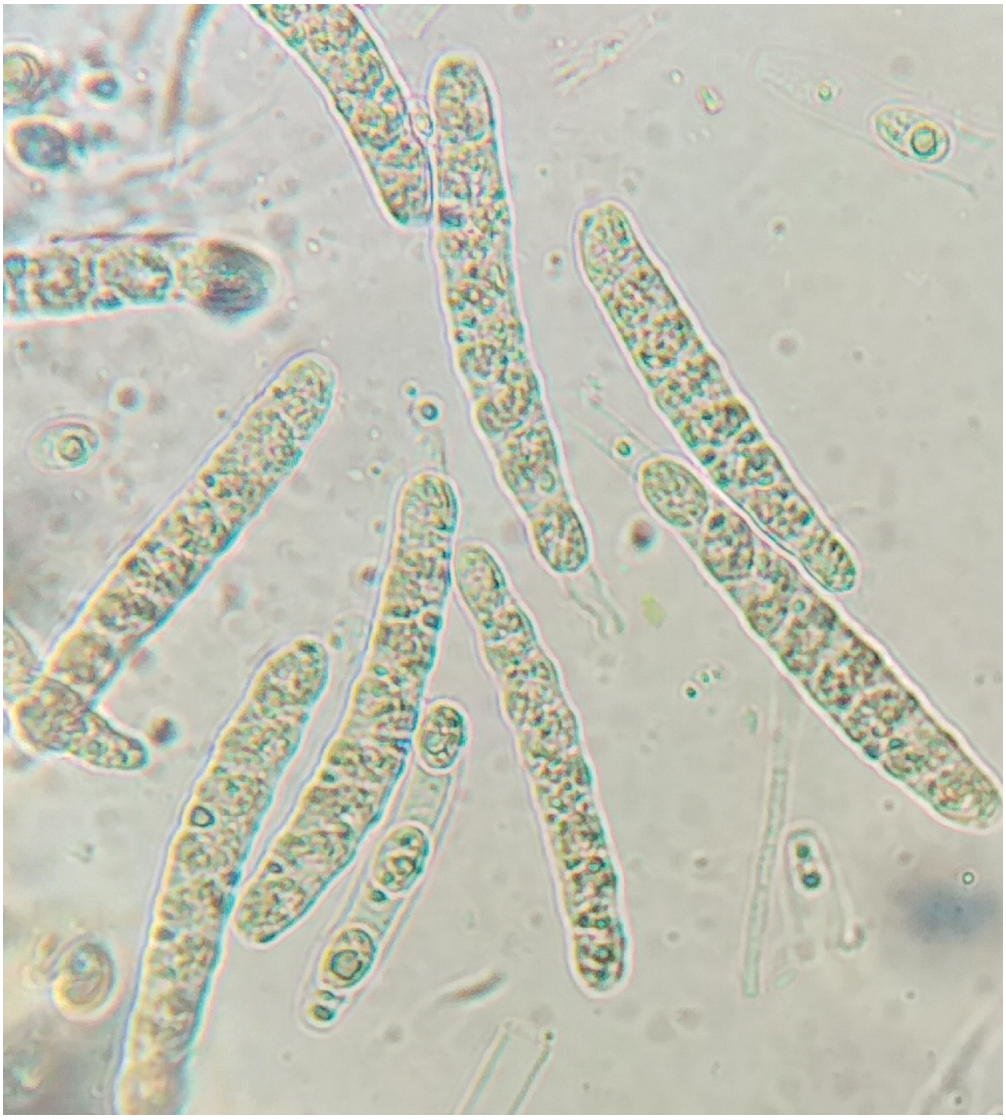
Slightly- raised, semi-circular, dark brown to black glossy structures known as stromata are shielded by clypeus.

82x91mm (300 x 300 DPI)



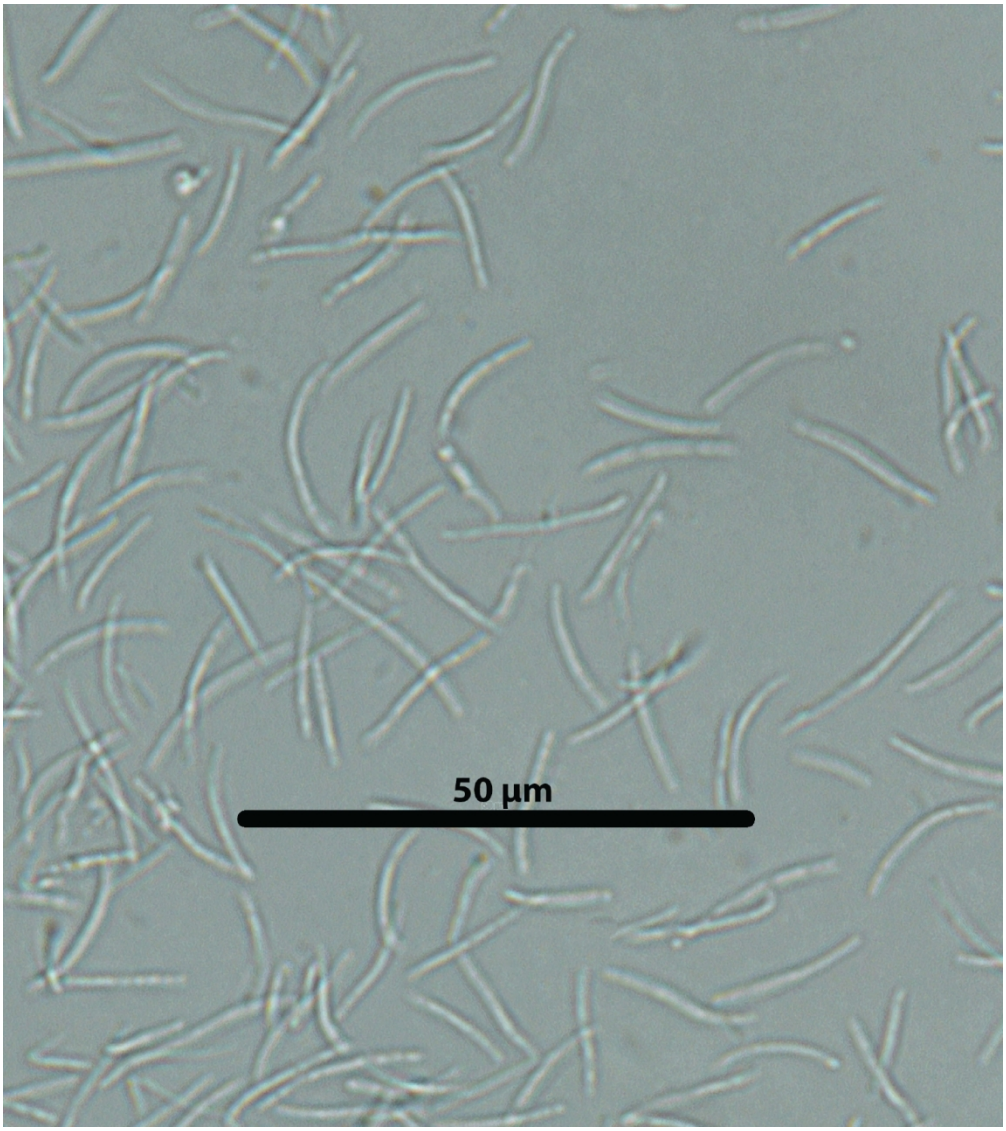
Stromata can be enclosed by brown, elliptic, necrotic halos known as "fisheye lesions" (indicated by arrows).

82x123mm (300 x 300 DPI)



Phyllachora maydis sexual spores (ascospores).

136x151mm (300 x 300 DPI)

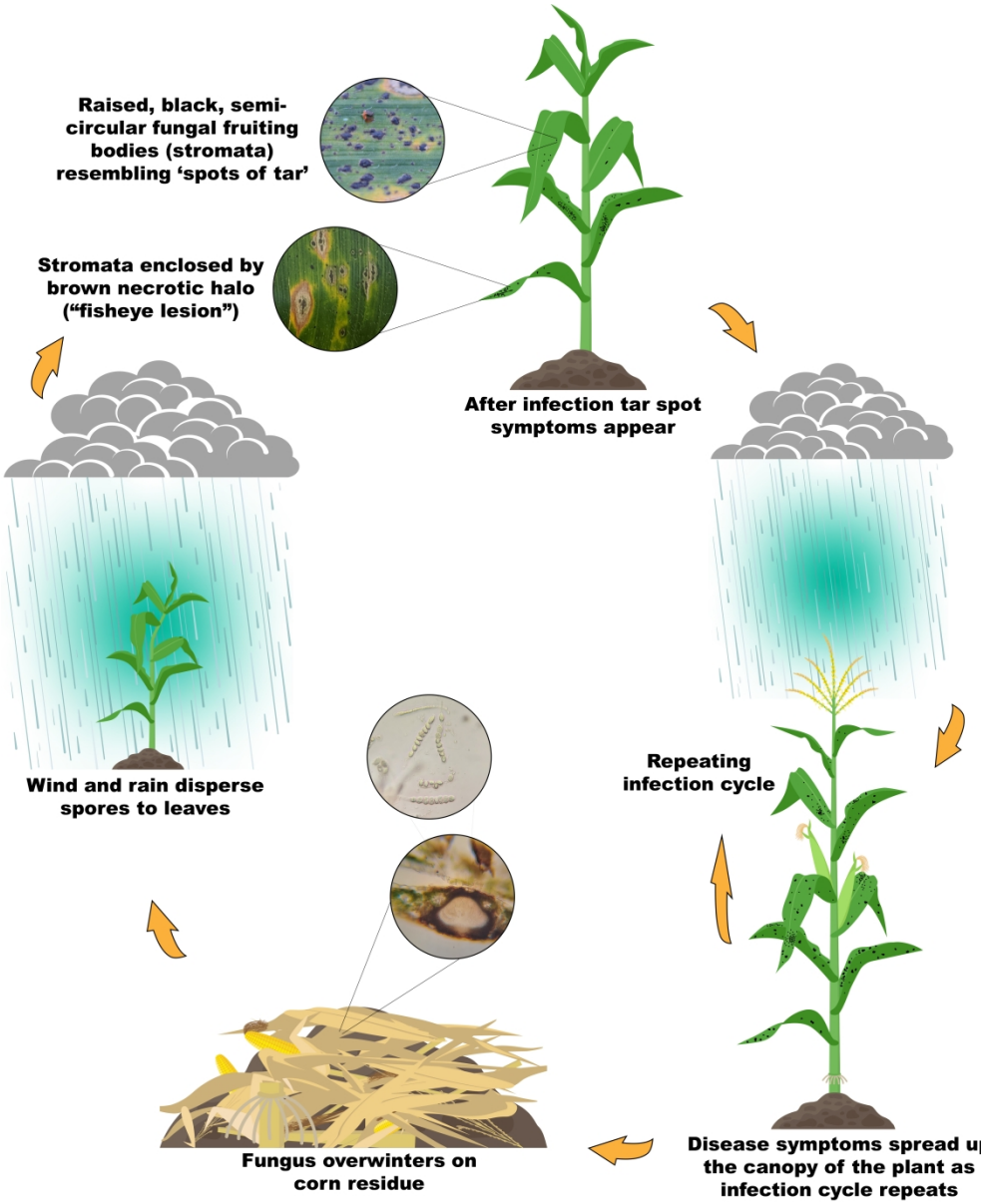


Phyllachora maydis asexual spores (conidia).

136x153mm (300 x 300 DPI)

Sexual spores (ascospores) of *Phyllachora maydis* can be discharged through a perithecial ostiole in a mucilaginous mass.

68x118mm (240 x 240 DPI)



Schematic representation of the presumed tar spot disease cycle in the United States. *Phyllachora maydis* is capable of overwintering in corn residue and generating secondary infections. Symptoms of tar spot can be observed 14 days after infection and new ascospores are produced in stromata soon thereafter. Ascospore dispersal has been documented to only as far as 31 m from source. However, anecdotal evidence suggests that long-distance dispersal may also occur.

370x445mm (300 x 300 DPI)

Phyllachora maydis was reported for the first time in Mexico in 1908 and currently is present in 14 additional countries. In the U.S. was reported in 2015, and is now established in nine states.

135x174mm (300 x 300 DPI)