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Diseases of Johnsongrass (*Sorghum halepense*): possible role as a reservoir of pathogens affecting other plants

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Review

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Abstract

Johnsongrass [*Sorghum halepense* (L.) Pers.] is one of the most noxious weeds distributed around the world. Due to its rapid growth, wide dissemination, seeds that can germinate after years in the soil, and ability to spread via rhizomes, *S. halepense* is difficult to control. From a perspective of plant pathology, *S. halepense* is also a potential reservoir of pathogens that can eventually jump to other crops, especially corn (*Zea mays* L.) and sorghum [*Sorghum bicolor* (L.) Moench]. As one of the most problematic weeds, *S. halepense* and its diseases can provide useful information concerning its role in diseases of agronomically important crops. An alternative consideration is that *S. halepense* may provide a source of genes for resistance to pathogens. While some studies have verified that pathogens isolated from *S. halepense* actually cause disease on host crops through cross inoculation, similarity of disease symptoms and pathogen morphology have been used for identity of the disease agent in most studies. Availability of DNA sequence information has greatly altered and improved pathogen identification, leading to significant changes in phylogenetic assignments. Reclassification of pathogens, especially fungi, raises new questions concerning the role of *S. halepense* as a disease reservoir. Our goals in this review are to pinpoint, where possible, diseases for which *S. halepense* acts as a significant pathogen reservoir and to point out problem areas where further research is needed.

Sorghum halepense and Diseases

Invasive plant species often dominate native species in competition (Schwinning et al. 2017). Among invasive plant species, Johnsongrass [*Sorghum halepense* (L.) Pers.], a wild relative of sorghum [*Sorghum bicolor* (L.) Moench], is known as an aggressive invader of natural or minimally managed habitats (Sezen et al. 2016).

After its introduction from the Mediterranean area into the United States in the 1800s, *S. halepense* was disseminated rapidly. By the late nineteenth century, its presence was almost nationwide, and its pernicious nature led to the first federal appropriation specifically for weed control in 1900 (McWhorter 1971).

By competing for resources, through allelopathy, and by serving as a host for crop pests, *S. halepense* can greatly diminish crop yield (Soti et al. 2020); for example, heavy infestations of *S. halepense* reduced the yield of soybean [*Glycine max* (L.) Merr.] in Mississippi 23% to 42% (McWhorter and Hartwig 1972). While it is generally considered a problem in corn (*Zea mays* L.), cotton (*Gossypium hirsutum* L.), and sugarcane (*Saccharum officinarum* L.) in tropical to temperate climates, 53 countries had reported it as a weed in 30 different crops by 1983 (Warwick and Black 1983). Furthermore, in the United States, tens of millions of dollars are attributed annually to management costs and yield losses (Burke et al. 2006).

Other concerns associated with *S. halepense* include the fact that weeds may be obligate alternate hosts for some pathogens, and herbicides used for weed control may interact with plant pathogens that might lead to a modified gene pool (Wisler and Norris 2005). Although *S. halepense* has been extensively studied in terms of its invasive properties and to discover potential methods of control, details about its diseases and potential roles as an alternate host for pathogens of major crops are lacking. We feel this review will be of interest to weed scientists, as it points out problems with earlier studies, especially as related to identification of species of pathogens, and the need and means that can be used to verify cross infection.

Sorghum halepense has been shown to serve as an alternative host for several insect pests of sorghum and corn, including sorghum midge [*Contarinia sorghicola* (Coquillett) (Diptera)], a leafhopper [*Graminella nigrifrons* (Forbes) (Homoptera)], and a corn leaf aphid [*Rhopalosiphum maidis* (Fitch) (Homoptera)] (Warwick and Black 1983), and many of the insects harbored in *S. halepense* may serve as vectors for diseases of crops such as maize chlorotic

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Table 1. List of fungal and oomycete pathogens found in *Sorghum halepense*, common hosts, and common names or symptoms of diseases.

Pathogen found in *S. halepense*	Common host(s)	Name of disease or common symptom	Original reference
Fungi			
Ascomycota			
Bipolaris cynodontis[a]	Bermudagrass[a]	Leaf spot	Pratt (2006)
Bipolaris spicifera[a]			
Bipolaris halepense	*S. halepense*	Leaf spot	Chiang et al. (1989a)
Bipolaris sorghicola	*Arabidopsis*, barley, onion, sorghum	Target leaf spot	Acciaresi and Mónaco (1999)
Claviceps africana	Sorghum	Ergot	Velasquez-Valle et al. (1998)
Colletotrichum sublineola[a]	Sorghum[a]	Anthracnose	Xavier et al. (2018)
Curvularia lunata	Corn, rice, sorghum, and more	Leaf spot Grain mold	Pratt (2006)
Curvularia geniculata	Corn	Leaf spot	Pratt (2006)
Exserohilum rostratum[a]	Bottle gourd, Pineapple, Rice, Bermudagrass[a]	Leaf spot	Pratt (2006)
Exserohilum turcicum[a]	Corn, sorghum	Northern corn leaf blight	Chiang et al. (1989b)
Gloeocercospora sorghi[a]	Sorghum	Zonate leaf spot	Chiang et al. (1989c)
Macrophomina phaseolina	Very wide host range cotton, sorghum, beans, etc.	Charcoal stalk rot, root rot	Khan (2007)
Ramulispora sorghicola	Sorghum	Oval leaf spot	Odvody et al. (2006)
Basidiomycota			
Rhizoctonia solani[b]	Turfgrass, soybean,[b] potato, rice, corn, sorghum	Brown patch, damping off, black scurf, root rot, stem rot, sheath blight of rice	Demirci and Eken (1999)
Rhizoctonia zeae	Turfgrass, corn	Brown patch, leaf spot	Demirci and Eken (1999)
Sporisorium cruentum[a] (*Sphacelotheca holci*)[a]	Sorghum[a]	Loose kernel smut	Massion and Lindow (1986)
Oomycetes			
Peronoscleospora sorghi	Sorghum	Downy mildew	Amador et al. (1974)

[a]Successful cross inoculation of isolates between host crop and *S. halepense*.
[b]Transfer onto *S. halepense* with an isolate from the host crop.

Table 2. List of bacterial pathogens found in *Sorghum halepense*, common hosts, and common name or symptoms of diseases.

Pathogen found in *S. halepense*	Common host(s)	Name of disease or common symptom	Original reference
Bacteria			
Clavibacter michiganensis[a]	Corn,[a] sugarcane, sorghum	Goss's wilt	Ikley et al. (2015)
Pseudomonas syringae	Wide range of monocots and dicots	Bacterial leaf spot	Mikulas and Sule (1979).
Rickettsia-like bacteria	Peach	Phony disease	Weaver et al. (1980)
Xanthomonas vasicola[b]	Corn[b]	Bacterial leaf streak	Hartman (2018)
Xylella fastidiosa[b]	Grape,[b] olive (*Olea europaea* L.)	Pierce's disease	Turner and Pollard (1959)

[a]Successful cross inoculation of isolates between host crop and *S. halepense*.
[b]Transfer onto *S. halepense* with an isolate from the host crop.

Table 3. List of viral pathogens found in *Sorghum halepense*, common hosts, and common name or symptoms of diseases.

Pathogen found in *S. halepense*	Common host(s)	Name of disease or common symptom	Original reference
Viruses			
S. halepense mosaic virus	Corn, sorghum	Chlorosis, stunting, mottling	Stewart et al. (2017)
Maize chlorotic dwarf virus	Corn, sorghum	Chlorosis, stunting, mottling	Stewart et al. (2014)
Maize dwarf mosaic virus	Corn, sorghum	Chlorosis, stunting, mottling	Stewart et al. (2014)
Sugarcane mosaic virus	Corn, sorghum	Chlorosis, stunting, mottling	Mohammadi et al. (2006)

dwarf virus (MCDV) and maize dwarf mosaic virus (MDMV) (King and Hagood 2003). However, in this review, we excluded information regarding insect pests other than those known to transmit viruses. Tables 1–3 summarize fungal, bacterial, and viral pathogens, respectively, that have been observed and verified to infect *S. halepense* and list other common hosts and common names of diseases caused by those pathogens.

Fungal Diseases of *Sorghum halepense*

Compared with other classes of pathogens, many fungi have been reported as pathogens of *S. halepense*. While sometimes mentioned as potential biocontrol organisms, their presence usually identifies *S. halepense* as a potential alternate host to a non-weed species. Here we will first consider fungi, especially ascomycetes, known to have a wide host range, and then consider those that exhibit a high degree of host specificity.

Ascomycota

Macrophomina phaseolina

An example of a pathogen with a very wide host range is *Macrophomina phaseolina* (Tassi) Goid. *Macrophomina phaseolina* has no known sexual stage. However, it is classed as an ascomycete based on the presence of DNA sequences for mating-type alleles (Nagel et al. 2018). It has been identified as the cause of charcoal rots in stem infections and damping off when roots are compromised for more than 500 wild and cultivated hosts,

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including *S. halepense* (Khan 2007). *Macrophomina phaseolina* is widely present in soil and has been reported to cause yield losses of 30% to 50% in southern soybean production regions of the United States (McGee 1992; Yang and Navi 2005). In sorghum, up to 46.6% yield loss was recorded for susceptible plants with complete wilting and lodging (Arora and Dhurwe 2014). In a study in Australia, *M. phaseolina* has been isolated from the roots of symptomless plants of 23 weed species, including *S. halepense* (Fuhlbohm et al. 2012). In a recent study of genetic diversity of *M. phaseolina* in Senegal based on DNA sequences of five loci, internal transcribed spacer (ITS), translation elongation factor (TEF), actin (ACT), calmodulin (CAL), and tubulin (TUB), two clades were generated, but no consistent correlation was found among genotype, host, or geographic location, and isolates from both clades could even occur on the same host at the same location (Sarr et al. 2014). Another recent study suggested that five *Macrophomina* species can be defined based on DNA sequence diversity among isolates collected from oilseed crops in Brazil (Machado et al. 2019). However, no indications for host specificity were described. Thus, while *S. halepense* could serve as a source of inoculum on occasion, it seems unlikely that it has a large impact on the overall spread of the crop diseases caused by *Macrophomina*.

Curvularia *spp. and* Bipolaris *spp.*

Curvularia lunata (Wakker) Boedijn and *Curvularia geniculata* (Tracy & Earle) Boedijn have been isolated from typical leaf spot lesions of a wide range of hosts, including *S. halepense* (Pratt 2006). No clear indication of host specificity has been seen. In a test to examine host range, single spore cultures of *C. lunata* isolated from lesions of the pulse black gram [*Vigna mungo* (L.) Hepper] were grown and used to prepare high concentrations of inoculum (Lal et al. 2013). When sprayed onto 30-d-old plants of 58 plant species in seven families, other than for the only three *Euphorbuaceae* species tested, at least one species in the other six families developed leaf spot symptoms. While *S. halepense* was not tested, corn and rice (*Oryza sativa* L.) were positive, but *Sorghum vulgare* (a synonym of *S. bicolor*) was negative (Lal et al. 2013). In other cases, *C. lunata* has been shown to cause leaf spot disease on grain sorghum in Pakistan (Akram et al. 2014) and on sweet sorghum in China (Tong et al. 2016), both of which are *S. bicolor*. *Curvularia lunata* is also often identified as a cause of grain mold in sorghum (Bandyopadhyay et al. 1991; Prom et al. 2017b). In corn, *C. lunata* is reported to cause approximately 10% to 60% yield losses and up to 33.4% losses in grain yield under hot and humid conditions (Bisht et al. 2018; DingFa et al. 1999).

Curvularia geniculata also causes leaf spot on corn and has previously been isolated from *S. halepense* (Hodges and Madsen 1979). Moreover, *C. lunata* and *C. geniculata* are associated with leaf spots of Lacatan banana (*Musa acuminata* Colla) plants (Meredith 1963). In a recent study, *C. geniculata* was confirmed as the principal alfalfa (*Medicago sativa* L.) foliar pathogen in the Brazilian state of Rio Grande do Sul (Ávila et al. 2017). Based on a survey conducted of seed-borne fungal diseases of rice in Burkina Faso, incidence rate of *C. geniculata* was 0.5% to 2% (Ouedraogo et al. 2016).

Bipolaris halepense Chiang, Leonard & Van Dyke was isolated from diseased leaves of *S. halepense* in North Carolina in 1989 (Chiang et al. 1989a). Conidia of *B. halepense* resemble those of *Bipolaris maydis* (Y. Nisik. & C. Miyake) Shoemaker, a foliar pathogen of corn, but *B. halepense* is only weakly pathogenic to corn and did not mate with fertile isolates of either mating type of *B. maydis* (Chiang et al. 1989a). Symptoms from *B. halepense* when found on *S. halepense* lack the zonate pattern, so are more typical for the lesions caused by *Bipolaris sorghicola* (Lefebre & Scherwin) Alcorn (Manamgoda et al. 2014). *B. sorghicola* was found on *S. halepense* in La Plata, Argentina, and the diseased *S. halepense* plants were described as having leaf spots (Acciaresi and Mónaco 1999). Katewa et al. (2006) inoculated conidia of *B. sorghicola* to sorghum cultivars 'IS164' and 'SU 45', and the reduction in grain yields was near 50% in both cultivars compared with the control.

Bipolaris sorghicola is reported to cause target leaf spot on barley (*Hordeum vulgare* L.), onion (*Allium cepa* L.), *Arabidopsis thaliana* spp., and sorghum (Peng et al. 2016).

In a 2006 report by Pratt, besides *C. lunata*, and *C. geniculata*, *Bipolaris cynodontis* (Marig.) Shoemaker, *Bipolaris spicifera* (Banier) Subr, and *Exserohilum rostratum* (Drechs.) Leonard & Suggs (formerly *Bipolaris halodes*) were also recovered from symptomatic leaves of *S. halepense*. In this case, the *S. halepense* was growing in association with Bermudagrass [*Cynodon dactylon* (L.) Pers.]. Spores produced from cultures of the two *Bipolaris* species and *E. rostatum* were cross-infective to Bermudagrass, causing typical leaf spot symptoms (Brecht et al. 2007; Pratt 2006). *Bipolaris cynodontis* has also been isolated from rice (Zehhar et al. 2008). In Bangladesh, the major pathogen of leaf blight in wheat (*Triticum aestivum* L.) is *Bipolaris sorokiniana* (Sacc.) Shoemaker, but other fungal species such as *Bipolaris cynodontis* (Marig.) Shoemaker, *Bipolaris oryzae* (Breda De Haan) Shoemaker, *Bipolaris tetramera* (Mckinney) Shoemaker, and *Bipolaris victoriae* (Meehan & Murphy) Shoemaker have been also isolated from infected wheat leaves (Momtaz et al. 2019). Although it is not proven to cause severe disease, *B. cynodontis* was found in 10.4% of the rice seed lots from a total of 722 rice seed lots in Rio Grande do Sul, Brazil (Meneses et al. 2014). As in the case of *Macrophomina*, even if *S. halepense* is a host for these pathogens, based on their extensive host ranges, it seems unlikely that it regularly serves as a major source of inoculum for this group of pathogens.

It is important to note that *C. lunata* refers to the asexually reproducing form (anamorph) of an ascomycetous fungus that also has a sexually reproducing form (teleomorph) in the genus *Cochliobolus*. Because identification of *Curvularia* based primarily on conidial morphology is not highly discriminatory, efforts are being made to use DNA sequence information to sort out the phylogeny of the group. Index Fungorum (http://www.indexfungorum.org/Names/Names.asp) lists 134 species of *Bipolaris*, 217 species of *Curvularia*, and 54 species of *Cochliobolus*, including *C. lunatus*, the presumed teleomorph of *C. lunata*. Several teleomorphs such as *Cochliobolus heterostrophus* (Drechsler) Drechsler are associated with serious diseases of specific hosts, including southern leaf blight of corn. When sequences of ribosomal ITS and a portion of the single-copy gene *g3pd* (glyceraldehyde-3-phosphate dehydrogenase, including 2 introns) for 41 species defined as *Cochliobolus* were subjected to phylogenetic analysis, the results grouped the isolates into two clusters (Berbee et al. 1999). For 16 species in cluster 2, the classification, if based on asexual spores, would be either *Curvularia* or *Bipolaris*. All species in cluster 1 (14 *Cochliobolus* species) were associated with *Bipolaris* as the anamorph. Addition of TEF and the large-subunit rRNA (LSU) sequences led to further reclassification of morphologically defined species of *Curvularia* and *Bipolaris* (Manamgoda 2015). In these studies, isolates from sorghum were classified into seven different species, none of which was *C. lunata* (Manamgoda 2015; Marin-Felix et al. 2020). Clearly, it will be important to use DNA sequence information to

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identify the species and to perform cross-species inoculation tests to determine whether *Curvularia* from *S. halepense* is a threat to neighboring crop species. The similarity of *Curvularia* and *Bipolaris* was not surprising, as each is known to derive from teleoforms of *Cochliobolus*. However, these observations show that isolates from different hosts described as separate species of *Curvularia* or *Bipolaris* in earlier literature may not meet today's species definitions. It is also possible that some are anamorphs derived from genetically distinct species that do have host specificity. (At one time these fungi were all classed as members of the genus *Helminthosporium* and later *Drechslera*.)

Exserohilum *spp.*

Exserohilum rostratum (or *Setosphaeria rostatum* when the name for the sexual stage is used), as stated previously, has been isolated from *S. halepense* and also appears to have a very wide host range. When *E. rostratum* isolates from banana were tested via assays using detached leaves from 128 different plant species belonging to 47 families, 60 developed leaf spot lesions. These included 17 of the 20 Gramineae tested, including corn (Lin et al. 2011). *Exserohilum rostratum* has been recovered from lesions on rice (Cardona and González 2007; Mahmad Toher et al. 2015), and it also causes leaf spot on bottle gourd [*Lagenaria siceraria* (Molina) Standl.] leaves (Choudhary et al. 2018) and pineapple (*Ananas comosus* (L.) Merr.] leaves (Luo et al. 2011). In July 2009, atypical symptoms of a leaf spot disease from which *E. rostratum* was cultured were observed on mature pineapple leaves in Chengmai County in China; approximately 15% of plants propagated from suckers became symptomatic after 150 to 300 d, eventually causing a 3% to 10% yield loss (Luo et al. 2011). *Exserohilum rostratum* has been implicated as causing root rot of lettuce (*Lactuca sativa* L.) (Alamri et al. 2019). Further, it is frequently mentioned as a pathogen in humans, as exemplified by Alajmi et al. (2019).

Based on results of greenhouse studies, a mixture of *Drechslera gigantea* (Heald & F.A. Wolf) S. Ito, *Exserohilum longirostratum* (Subram.) *Sivan*, and *E. rostratum* has been recommended as a biocontrol for *S. halepense* and six other weed species (Chandramohan and Charudattan 2001). The tests included inoculation of seedlings of six sorghum and six corn varieties as well as other garden and crop species that were all either resistant or immune. No follow-up reports on in-field applications were found.

Once again, the use of DNA sequence information, in this case from nine different regions, has led to significant reevaluation of *Exserohilum* spp. Most notably, *E. rostratum* was revealed as conspecific with other previously described *Exserohilum* species such as *Exserohilum antillanum* R.F. Castañeda, Guarro & Cano, *Exserohilum gedarefense* (El Shafie) Alcorn, *Exserohilum leptochloae* Y. Nisik. & C. Miyake, *Exserohilum longirostratum* (Subram.) Sivan., *Exserohilum macginnisii* A.A. Padhye & Ajello, and *Exserohilum prolatum* K.J. Leonard & Suggs. Isolates from sorghum still fell into seven different species, most commonly *Exserohilum turcicum* (Pass.) Leonard & Sugg. (Hernández-Restrepo et al. 2018).

Exserohilum turcicum is most widely known as the cause of northern corn leaf blight in corn (Chiang et al. 1989b). It is one of the most common and economically significant fungal leaf diseases of corn in the north-central United States and Ontario, Canada (Jindal et al. 2019; Weems and Bradley 2017), and this destructive pathogen can reduce the grain yield of corn by more than 90% (Pant et al. 2000). Other studies have shown mixed results as far as host specificity of isolates. Reports describing recovery from *S. halepense* include Chiang et al. (1989b), who found that *S. halepense* seedlings are susceptible to isolates recovered from *Sorghum* spp. (Sudan grass [*Sorghum bicolor* (L.) Moench ssp. *drummondi* (Nees ex Steud.) de Wet & Harlan], *S. halepense*, and broomcorn [*Sorghum vulgare* Pers. var. *technicum* (Koern.) Jáv.]); *S. halepense* has been identified as an overwintering host (Levy 1984). It can also provide a suitable medium in culture for crosses involving the teleomorph (*Setosphaeria turcica*) (Moghaddam and Pataky 1994). Sorghum host differentials have been identified in India that show varying responses across locations, indicating that multiple pathotypes are present (Mathur et al. 2011). However, lack of cross infection between corn and *S. halepense* isolates has also been reported (Abadi et al. 1996). In one study, an *E. turcicum* originally isolated from *S. halepense* in Italy was inoculated to 40 varieties of cultivated sorghum, 25 hybrids of corn, and 5 varieties of durum wheat, bread wheat, oat (*Avena sativa* L.), barley and rice. Overall, only 15 varieties of cultivated sorghum showed a mild level of infection (Del Serrone and Fornasari 1995). In a similar study, a North Carolina isolate of *E. turcicum* that had been isolated from *S. halepense* caused moderate to severe damage to sorghum and corn (Chiang et al. 1989c). So, *S. halepense* may well act as a significant reservoir for *E. turcicum*.

Claviceps Africana

Sorghum ergot, caused by *Claviceps africana* Frederickson, Mantle & De Milliano, is a disease that replaces the seed on panicles of infected florets with sphacelia/sclerotia (Odvody et al. 2002). In India, losses of 10% to 80% have been reported in hybrid seed production fields, and ergot epiphytotics in Zimbabwe result in regular annual losses of 12% to 25% and occasionally in total losses (Bandyopadhyay et al. 1998). Although now global in nature, sorghum ergot was not known to be in the Western Hemisphere before 1995. After being reported in Mexico (Velasquez-Valle et al. 1998), it was later seen in Texas in the lower Rio Grande valley, where it was found in both sorghum fields and adjacent stands of *S. halepense* (Isakeit et al. 2007). Because of the mild climate in the Rio Grande region, conidia can be produced year-round, providing a continual source of inoculum. Consequently, *S. halepense* has been suggested as a likely source of recurring disease (Odvody and Isaskeit 1997; Prom et al. 2005), allowing annual spread throughout U.S. sorghum production regions as the growing season advances northward.

Sporisorium cruentum

In a greenhouse study, teliospores of *Sphacelotheca holci* Jack. [= *Sphaceloiheca cruenta* (Kühn.) Potter] (synonym to *Sporisorium cruentum* (Kühn) K. Vánky), that causes loose kernel smut in sorghum, infected *S. halepense* systemically after inoculation of cut stems (Massion and Lindow 1986). *S. cruentum* has been suggested as a biological control for *S. halepense* (Millhollon 2000), but isolates from *S. halepense* also cause loose kernel smut in sorghum as reported by Dean (1966). Recently, a sample from *S. halepense* was shown to readily infect sorghum cultivar 'BTx643' plants (Prom et al. 2017a), making any use to control *S. halepense* a potential problem for nearby sorghum. In Ethiopia, the incidence of covered kernel smut is estimated to be around 50% (Azanaw et al. 2020; Mengistu 1982).

Colletotrichum sublineola

Before 1992 (and sometimes since) the species name *graminicola* was used to identify pathogens in the genus *Colletotrichum* that cause anthracnose on corn, sorghum, and other gramineae crops,

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with some isolates being identified as having restricted host specificity. However, based on differences between perfect stages (*Glomerella*) (Vaillancourt and Hanau 1992) and ITS sequencing (Sherriff et al. 1995), *Colletotrichum sublineola* Henn. ex Sacc. & Trotter 1913 (or *sublineolum*) is now used for isolates that infect sorghum. *Sorghum halepense* isolates of *C. sublineola*, have been shown to infect sorghum cultivars (Xavier et al. 2018). Conversely, under ideal conditions in a greenhouse, only inoculation at late growth stages of *S. halepense* led to infection by *C. sublineola* isolates originating from grain sorghum (Ahn et al. 2020). In 1989, it was reported that *C. graminicola* extracted from *S. halepense* caused moderate to severe leaf damage on corn and sorghum; even oats and barley were slightly affected by this isolate (Chiang et al. 1989c). However, this was before the separation of the species names *graminicola* and *sublineola* in 1992, so the identity of the *Colletotrichum* isolate used in the study is not clear, nor is it known whether other species also can reproduce on *S. halepense*. In sorghum, losses caused by the panicle phase of anthracnose in terms of grain yield are generally 2% to 15% but may be up to 30% to 50% (Frederiksen and Odvody 2000), so *S. halepense* and possible other alternate hosts do pose a potential threat for sorghum production.

Gloeocercospora sorghi

Gloeocercospora sorghi Bain & Edgerton causes zonate leaf spot on sorghum and has been recovered from *S. halepense* showing the same symptoms (Chiang et al. 1989a). Inoculation with an isolate of *G. sorghi* from *S. halepense* caused damage to corn and sorghum; mycelial growth and sclerotia appeared on incubated leaves of *Sorghum* spp. but not other species, which indicates that *G. sorghi* was compatible only with *Sorghum* spp. (Chiang et al. 1989c). Although the distinctive pattern of infection of sorghum leaves show it is a very common disease, it seems not to cause sufficient levels of yield loss to stimulate further research. *Gloeocercospora sorghi* has been tested as bioherbicide for *S. halepense* (Mitchell et al. 2003), but the paper also pointed out it was highly virulent in other sorghums.

Ramulispora sorghicola

Oval leaf spot caused by *Ramulispora sorghicola* E. Harris was observed on sorghum and *S. halepense* near Beeville, TX, during August 2002 (Odvody et al. 2006). The observation that rows of sorghum nearest to *S. halepense* displayed the same symptoms and that conidial cultures were found to reproduce the disease on both hosts implies that *S. halepense* was serving as a spreader. In winter months, oval leaf spot was mostly found on *S. halepense*, further strengthening the idea that *S. halepense* was the primary source. Because resistant sorghum cultivars are available, *R. sorghicola* has not led to significant sorghum yield losses (Odvody et al. 2006).

Basidiomycota

A few fungal pathogens of *S. halepense* are categorized in phylum basidiomycota.

Rhizoctonia solani

Rhizoctonia solani Kühn [teleomorph *Thanatephorus cucumeris* (A.B. Frank) Donk.], an undefined binucleate *Rhizoctonia*, and *Rhizoctonia zeae* Voorhees (teleomorph *Waitea circinata* Warcup & Talbot AG Z) were isolated from *S. halepense* growing in Turkey (Demirci and Eken 1999; Demirci et al. 2002). *Rhizoctonia solani* is a soilborne plant pathogen with considerable diversity in cultural morphology, host range, and aggressiveness (Ajayi-Oyetunde and Bradley 2018). Heterokaryon compatibility subdivides the species into 14 anastomosis groups that may differ in host range, several of which (AG-1A AG1B, AG4, and AG-5) have been isolated from corn (Li et al. 1998) and, except for AG-1B, from sorghum (Gao 1987). AG-1 isolates are also pathogens of soybean, and soybean isolates have been shown to infect *S. halepense* (Black et al. 1996). The *R. solani* that causes severe seedling damping-off up to 80% to 100% and final yield loss of up to 30% of oilseed rape (*Brassica napus* L.) worldwide belongs to AG2-1 (Kataria and Verma 1992; Khangura et al. 1999; Sturrock et al. 2015; Tahvonen et al. 1984).

While *R. zeae* derives its name from a corn disease described in 1934 (Voorhees 1934), it has also been reported to infect turfgrass in Florida, Ohio, and Ontario (Elliott 1999; Hsiang and Masilamany 2007) and rice (Sifat and Monjil 2017). More research is required to determine whether *S. halepense* serves as a source of *Rhizoctonia* diseases of crop species and, if so, which of the anastomosis groups are involved.

Sporisorium reilianum

Sporisorium reilianum (J.G. Kühn) Langdon & Full. (formerly *Sphacelothca reiliana*), the cause of head smut in sorghum and corn, may represent an exception where *S. halepense* is not a host. Yield losses attributed to *S. reilianum* are estimated to be as high as 80% in corn (Frederiksen 1977; Jin et al. 2000; Yu et al. 2014). Attempts to create infections using sporidia from cultures derived from teliospores collected from infected sorghum did not produce infection from spray, needle, or root-dip inoculation on any of several *S. halepense* cultivars tested (personal observations).

Bacterial Diseases of *Sorghum halepense*

More than 2,000 bacterial species have been reported as pathogens to more than 2,500 species of various plant hosts (Frederiksen and Odvody 2000). Among them, relatively few bacterial pathogens are known to be harbored in *S. halepense*.

Clavibacter michiganensis

Clavibacter michiganensis subsp. *nebraskensis* (Cmn), causal agent of Goss's wilt of corn, sugarcane, and sorghum, can also infect *S. halepense*, which confirms that *S. halepense* may serve as alternate host (Ikley et al. 2015). In this case, plants were inoculated with a sample originally from corn. Bacteria from resulting lesions were isolated and verified via Agdia® immunostrips specific for Cmn, and Koch's postulates were fulfilled by showing pathogenicity on corn. Disease incidence in affected cornfields ranged from 20% to 60%, and significant yield loss was reported (Ruhl et al. 2009). Spread from *S. halepense* to corn or other crops could severely reduce yield.

Pseudomonas syringae

Pseudomonas syringae Van Hall was recovered from a lesion on a *S. halepense* leaf that caused circular to ellipsoidal, tan-orange-red to blackish-purple spots (Mikulas and Sule 1979). Bacterial leaf spot has not been reported to be of widespread occurrence in sorghum, so control measures are not likely to be warranted (Frederiksen and Odvody 2000).

Rickettsia-like Bacteria

Rickettsia-like bacteria (RLB) were consistently observed in KOH extracts of *S. halepense* stems collected in peach [*Prunus persica*

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(L.) Batsch] orchards with Phony disease. Although the RLB from *S. halepense* could not be cultured, it was antigenically similar to the RLB from infected peach trees, and its high incidence in orchards with Phony disease suggested a potential causal association through transmission via leafhoppers (Weaver et al. 1980).

Xanthomonas vasicola

Xanthomonas vasicola pv. *Vasculorum* causes bacterial leaf streak in corn, and in a recent study, it was revealed that *S. halepense* is an alternative host of *X. vasicola* (Hartman 2018). That study also showed that cultivars of grain sorghum, oats, and rice also developed symptoms when inoculated with bacterial cultures grown from a corn isolate. The same bacterium is known to cause gummy disease of sugarcane (Hartman 2018). The impact of bacterial leaf streak on yield is not yet known, but it is not considered a major disease on crops (Byamukama et al. 2020).

Xylella fastidiosa

Xylella fastidiosa, a common bacterial pathogen that causes Pierce's disease in grapes (*Vitis aestivalis* Michx.), was found in *S. halepense* in 1959 (Turner and Pollard 1959). More recently, inoculation of weed species with sharpshooter insects [*Homalodisca vitripennis* (Germar), formerly known as *H. coagulate* (Say); *Xyphon fulgidum* (Nottingham); and *Graphocephala atropunctata* (Signoret)] previously fed on infected grapes for 4 d found that 14 of 62 inoculated *S. halepense* plants maintained detectable levels of the pathogen, with systemic spread in two of the plants (Wistrom and Purcell 2005). However, an assay made the following year showed that many other weeds in almond [*Prunus dulcis* (Mill.) D.A. Webb] orchards in the same region also harbored *X. fastidiosa*, and in that survey, no positive tests were found on *S. halepense* (Shapland et al. 2006).

The cost of Pierce's disease in California is approximately \$104.4 million yr^{-1} (Tumber et al. 2014), so weed as well as insect control measures are warranted.

Viral Diseases of *Sorghum halepense*

A 1965 report of a virus found on *S. halepense* in California assumed it came from nearby sugarcane, and although it had some serologic cross reactions, it was found to be indistinguishable from maize mosaic virus (MMV) and in fact was not infectious to sugarcane (Shephard 1965).

Sorghum halepense Mosaic Virus

Johnsongrass mosaic virus (JGMV), now recognized as a member of a family of potyviruses, infects corn, sorghum, and *S. halepense* but not wheat or oat (Stewart et al. 2017). The JGMV complete RNA genome sequence in GenBank is 9,779-bases long. While antibody-based tests can differentiate JGMV, SCMV (sugarcane), MDMV (maize dwarf), and SrMV (sorghum) as being antigenically distinct (McKern et al. 1990), comparisons of the polyprotein or coat protein amino acid sequences show significant similarity to one another and also to *Pennisetum* mosaic virus (Laidlaw et al. 2004). JGMV does not show high similarity to MMV, which is larger, at 12,133 nucleotides. Recently, JGMV has been implicated as the sole (Stewart et al. 2017) or as a participating (Redinbaugh and Stewart 2018) virus component in a disease called maize lethal necrosis, a serious emerging disease on corn in East Africa.

Maize Dwarf Mosaic Virus and Maize Chlorotic Dwarf Virus

Two major U.S. corn viruses, MDMV and MCDV, can also be isolated from *S. halepense*. A virus disease problem emerged in southern Ohio and surrounding regions in the 1960s (Stewart et al. 2014). MDMV caused up to 70% loss in corn yield globally since the 1960s (Kannan et al. 2018). Similarly, MCDV is known to cause significant height (34% average) and yield reductions (72% average) (Louie et al. 1990). Spread of MDMV from introduced virus-infected *S. halepense* to adjacent susceptible corn in experimental plots was evaluated during 1979 and 1980 (Knoke et al. 1983). Field experiments were conducted to evaluate the hypothesis that *S. halepense* control in corn causes increased MDMV and MCDV disease severity because of increased movement of insect vectors from dying *S. halepense* to the corn crop (Eberwine and Hagood 1995). In a follow-up study that took advantage of newer technology, reverse transcriptase sequencing reads made from RNA extracts of *S. halepense* and corn in the same region of southern Ohio, MDMV, MCDV, SCMV, SrMV, and MCMV sequences were found in both hosts, but JGMV was not detected (Stewart et al. 2014). MDMV was also detected on *S. halepense* in Oklahoma (Wijayasekara and Ali 2017). In earlier studies, the leafhopper vector was allowed to acquire MCDV from corn or *S. halepense* source plants positioned in the center of corn plots. Results showed that spread from *S. halepense* was lower than if the insects fed on infected corn (Rodriguez et al. 1993).

Sugarcane Mosaic Virus

Sugarcane mosaic virus (SCMV), a causal agent of mosaic and dwarf mosaic on corn, sugarcane, and sorghum, was prevalent on *S. halepense* in marginal areas of cornfields (Mohammadi et al. 2006). SCMV, which is considered as one of the top 10 most economically damaging plant viruses, reduces sorghum and sugarcane yields around 10% to 35% and corn yield around 20% to 50% (Braidwood et al. 2019; Rybicki 2015; Viswanathan and Balamuralikrishnan 2005; Zhu et al. 2014), so removing *S. halepense* around fields is warranted.

Oomycete Diseases of *Sorghum halepense*

Peronoscleospora sorghi

Sorghum downy mildew, incited by *Peronoscleospora sorghi* (Weston and Uppal) C.G. Shaw, has been known for almost 50 yr to be pathogenic to *S. halepense* (Amador et al. 1974). In 2000, it was observed on corn, sorghum, and *S. halepense* in Uganda (Bigirwa et al. 2000). In that report, cross inoculation was demonstrated for spores taken from each host, but the symptoms were least on corn. However, within the southern epidemic zone in Nigeria, Zimbabwe, Zambia, Mozambique, and Rwanda, yield loss of corn was estimated to be 11.7%; individual fields had up to 95% incidence of systemically infected plants (Bock et al. 1998). Pathotypes of *P. sorghi* have been defined based on differences in host differentials in sorghum, but no similar tests have been reported for *S. halepense*.

Current Mainstream Technologies for Studying Diseases in *Sorghum halepense*

Sorghum halepense has been both a known and suspected reservoir of pathogens that have potential to cause diseases in other crops. Understanding of diseases of *S. halepense* that can potentially

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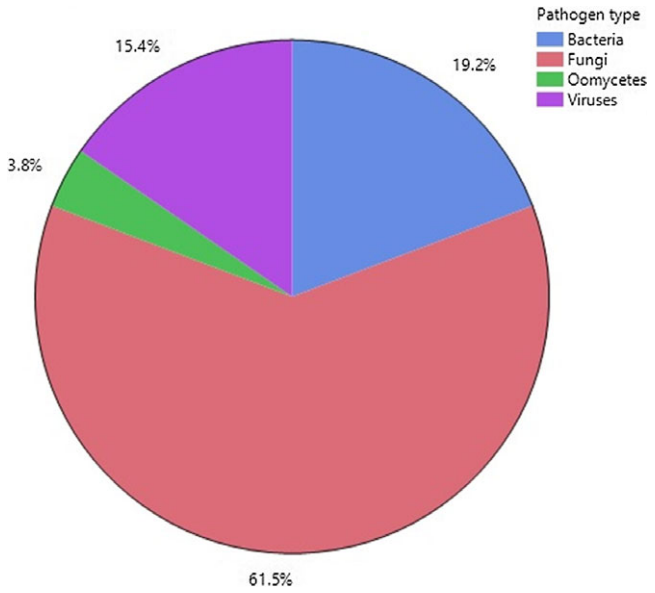


Figure 1. A pie chart that summarizes the proportions of the four categories of pathogens found in *Sorghum halepense*. Percentages displayed are rounded to the nearest tenth of a percent, and therefore do not total 100%.

cross-infect agronomically important crops can provide valuable information for crop protection against the pathogens. Among four types of pathogens, fungal pathogens for other host plants were most frequently detected in *S. halepense* (Figure 1). As would be predicted based on their close phylogenetic relationship based on DNA sequencing, sorghum pathogens were more frequently found in *S. halepense* compared with pathogens of other crops. However, many of those same pathogens have also been found on other weeds, and only a few studies have been made since the advent of DNA-based sequence information, which can be used to more accurately define species or strains showing host specificity. Likewise, essentially no studies have investigated the infection process or reproductive cycle of pathogens of *S. halepense*. As a consequence, for most pathogens, the role of *S. halepense* as a reservoir remains to be investigated. Recent studies of based on real-time qRT-PCR analysis using primers designed for sorghum genes found upregulated defense-related genes in *S. halepense* when inoculated with *C. sublineola* (Ahn et al. 2018). Although never directly applied to *S. halepense*, recent technologies such as genome-wide association studies (GWAS) and RNA sequencing (RNA-seq) are expected to be applied in *S. halepense* to study diseases of *S. halepense* and their responses to various pathogens.

Potential for Using Diseases of *Sorghum halepense* for Its Biological Control

As indicated earlier, several pathogens such as *S. cruentum*, *G. sorghi*, and a mix of three fungal pathogens (*D. gigantea*, *E. longirostratum*, and *E. rostratum*) have been studied or even recommended as biocontrol agents (Chandramohan and Charudattan 2001; Millhollon 2000; Mitchell et al. 2003). In some cases, the pathogens have later been found to cause disease in at least some cultivars of sorghum or, as in the case of *G. sorghi*, *S. halepense* was found to regrow after initial damage, a likely result from sprouting of rhizomes. *Sorghum halepense* rhizomes are known to allow pathogens such as MDMV to overwinter (Williams et al. 1966). Also, sorghum and *S. halepense* seedlings may contain high levels of dhurrin, a cyanogenic glucoside that may contribute to juvenile resistance to pathogens and insects (Ahn et al. 2020). Consequently, use of plant pathogens for inoculation at multiple stages of plant growth may be required for confirmation. For example, when 21 and 26 *S. halepense* cultivars grown in a greenhouse were inoculated at the 8-leaf stage with *C. sublineola* isolates FSP35 and FSP53, respectively, which are highly virulent on sorghum, no lesion with acervuli formation was found (Ahn et al. 2018, 2020). However, when the same 21 *S. halepense* cultivars were inoculated post-heading with FSP35, high numbers of sporulating lesions were present (Ahn et al. 2020). The appearance of symptoms does not guarantee pathogen reproduction has occurred and thus cannot be taken as proof of transmission in either direction, because avirulent strains of a pathogen, or even non-pathogens, may induce defense reactions that have visible symptoms, even though the pathogen does not produce infective propagules.

Potential for Leveraging *Sorghum halepense* Disease-Resistant Genes for Crop Trait Development

Based on real-time qRT-PCR analysis using primers designed for sorghum genes, *S. halepense* has been shown to upregulate defense-related genes, including *chalcone synthase 8*, *thaumatin-like protein*, and *flavonoid-3′-hydroxylase*, when inoculated with *C. sublineola* (Ahn et al. 2018; Ahn et al. 2019b). Bermudagrass southern mosaic virus (BgSMV), a nonpathogenic virus to *S. halepense*, triggered genes related to plant defense responses, including *nonexpressor of pathogenesis related genes 1* (*NPR1*), *peroxiredoxin*, and *S-adenosyl methionine synthase* (*SAM*), to higher levels than in *S. halepense* plants inoculated with MDMV (Mostafavi et al. 2019). In sorghum, nonpathogenic fungi have been known to activate defense-related genes of sorghum with distinctive patterns that are comparable to patterns caused by pathogenic fungi (Lo et al. 1999). Xavier et al. (2018) reported that *C. sublineola* isolates collected from *S. halepense* are phylogenetically distinctive from the isolates collected from sorghum. Therefore, distinct patterns of defense-related gene expression are expected when sorghums are inoculated with *C. sublineola* isolates collected from *S. halepense*.

Sorghum halepense may provide a source of genes for resistance to pathogens. As a tetraploid that evolved from hybridization between *S. bicolor* and *Sorghum propinquum* (Kunth) Hitchc. around 96 million years ago (Paterson et al. 2020), *S. halepense* is expected to have duplicates of many genes, including resistance R genes that trigger response to effectors from a potential pathogen. Not only are there more R genes present, but it is likely that a change in an R gene in one genome would not lead to loss of response to a specific elicitor because of the orthologous gene in the other genome. While mapping of R genes has not been carried out in *S. halepense*, progress is being made in sorghum, in which DNA-based tags for R genes and defense response genes are being identified. In sorghum, GWAS have been used to identify defense-related single-nucleotide polymorphisms (SNPs) to pathogens such as *C. sublineola* (Ahn et al. 2019a; Cuevas et al. 2018; Prom et al. 2019) and *E. turcicum* (Ding et al. 2015; Zhang et al. 2020). As more of these genes become identified, it will be interesting to compare both gene sequences and levels of expression following inoculation with a pathogen. It will also be interesting to identify putative R genes in *S. halepense* that differ from those in sorghum, as they could provide a source of ready-made

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resistance suitable for transfer to other crops, especially if the gene product can be shown to interact with a specific elicitor.

Future Research Directions

Diseases of *S. halepense* have not been extensively explored, and there are unknown pathogens of *S. halepense* as well (personal observations). Future research should take advantage of DNA sequence information for identification of species, and even pathotypes, when testing cross infection of potential pathogens that may transfer between major crops and *S. halepense*.

In summary, while *S. halepense* shares many pathogens with important crops, proof of a role in crop disease in many cases remains elusive. Factors that must be considered include:

1. Verification of the species causing disease in both hosts by successful cross inoculation and recovery, as backed up by DNA sequence information. This would also eliminate nearly identical pathogens that have developed host specificity through coevolution with the different hosts.
2. Because environmental conditions, including plant developmental stage, are critical for successful pathogen reproduction, tests must be made in conducive environments and at multiple stages of plant growth. In the meantime, eliminating *S. halepense*, especially stands growing near sorghum, is important.

Overall Lessons

Sorghum halepense is one of the most problematic weeds in the world due to rapid growth and wide dispersal of seeds and rhizomes. In addition, it is clear that *S. halepense* carries fungal, bacterial, viral, and oomycete pathogens that may infect other crops. However, in many studies, rigorous proof that it is the same pathogen is lacking, a problem that can now be addressed using DNA sequence information.

As for future research directions, possible suggestions include studies to identify possible genes for resistance, either broadscale or to specific races of fungal pathogens, which are areas that have not been explored because *S. halepense* is a weed. Despite the fact that diseases of *S. halepense* are not well studied, it is essential to understand that *S. halepense* could spread known and possible unknown diseases to other crops. Also, if it is possible to find strains of pathogens that heavily damage *S. halepense* but cause no/mild symptom(s) in other plants, it may be possible to use these pathogens as biocontrol agents. Further, genes from *S. halepense* that trigger hypersensitive responses to various pathogens may be useful in creating improved pathogen resistance in crops such as sorghum by interspecific crosses or gene transfer and editing technologies.

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