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REVIEW

New Approaches to an Old Problem: Dollar Spot of Turfgrass

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ABSTRACT

Dollar spot, caused by fungal pathogens *Clarireedia* spp. (formerly *Sclerotinia homoeocarpa*), is the most common and widely distributed disease of turfgrass worldwide. It can drastically reduce the quality of turfgrass species and affect their aesthetic value and playability. Management of dollar spot typically includes a costly program of multiple application of fungicides within a growing season. Consequently, there have been reported cases of fungicide resistance in populations of *Clarireedia* spp. Host resistance could be an important component of dollar spot management; however, this approach has been hampered by the lack of sources of resistance because nearly all known warm- and cool-season turfgrass species are susceptible. With the recent advancement in genome sequencing technologies, studies on pathogen genomics and host–pathogen interactions are emerging with the hope of revealing candidate resistance genes in turfgrass and genes for virulence and pathogenicity in *Clarireedia* spp. Large-scale screening of turfgrass germplasm and quantitative trait locus (QTL) analysis for dollar spot resistance are important for resistance breeding, but only a handful of such studies have been conducted to date. This review summarizes currently available information on the dollar spot pathosystem, taxonomy, pathogen genomics, host–pathogen interaction, genetics of resistance, and QTL mapping and also provides some thoughts for future research prospects to better manage this disease.

Keywords: *Clarireedia* spp., dollar spot, genetic resistance, genome, quantitative trait loci, turfgrass

Turfgrass has been used for centuries for recreational activities and is a valuable economic commodity in the United States and worldwide (Haydu et al. 2006). The total land covered by turfgrass in the United States is estimated to be >8.1 million hectares on home lawns, golf courses, and other areas, which places turfgrass third in total agricultural crop acreage nationwide (Breuninger et al. 2013; Morris 2003). Well-maintained turfgrass also provides important environmental benefits including improved groundwater recharge and surface water quality, reduced soil erosion, dust abatement, increased soil carbon sequestration, and reduced noise (Held and Potter 2012).

Maintaining turfgrass to a level of high aesthetic quality and playability often depends on successful disease management (Smiley et al. 2005; Walsh et al. 1999). Turfgrass species are affected by only a handful of plant pathogens, but by far, dollar spot is the most common and widely distributed disease of all warm-season (C4) and cool-season (C3) grasses worldwide (Goodman and Burpee 1991). Dollar spot has been observed in all areas where turf is grown, including golf courses, home lawns, and athletic fields (Mitkowski and Colucci 2006), and it has been documented most extensively in North America, Europe, and Australasia (Viji et al. 2004). Typical symptoms of dollar spot include white to straw-colored lesions that progress across leaf blades and move downward from the leaf tip. As the disease progresses, circular, sunken patches appear with varying diameters. The circular patches resemble silver dollars, hence the name *dollar spot* (Bennett 1937). Several cultural practices have been found effective in reducing dollar spot, but fungicides are often needed to provide effective control (Walsh et al. 1999). More money is spent annually on chemicals to control dollar spot than any other turfgrass disease (Vargas 2005). Genetic resistance is one way control dollar spot; however, highly resistant or immune cultivars to this pathogen are lacking in most turfgrass species (Steketee et al. 2017).

Taxonomy of the fungal pathogen causing dollar spot of turfgrass has been confusing and a subject of debate for eight decades (Salgado-Salazar et al. 2018). The fungal pathogen was first described in 1937 as the ascomycete *Sclerotinia homoeocarpa*

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(Bennett 1937). Since then, advancements in various molecular and morphological techniques have provided new insights into a more appropriate classification and nomenclature of this pathogen. By using DNA sequencing data of isolates collected from different parts of the world, Salgado-Salazar et al. (2018) reclassified *S. homoeocarpa* into a new genus of the family *Rutstroemiaceae*, *Clarireedia*, with four different species.

In this review, we summarize currently available knowledge on dollar spot and its causal agent *Clarireedia* spp. This review will be beneficial for the turfgrass scientific community in acquiring a broad range of knowledge on disease epidemiology and management and providing information useful for the development of turfgrass germplasm with improved dollar spot resistance.

DISEASE IMPORTANCE, SYMPTOMS, AND EPIDEMIOLOGY

In the United States, the turfgrass industry contributes >822,849 jobs and has a total economic impact of US$57.9 billion annually (Haydu et al. 2006). Because of high demands in aesthetic quality and playability, mitigating dollar spot is a major expense for the turfgrass industry. In nontreated turfgrass plots, dollar spot can reach 90% disease severity. Controlling foliar diseases on golf courses comes at an average cost of US$15,000 per golf course per year (the equivalent of 10 fungicide treatments a year). Studies have demonstrated that more money is spent on fungicide every year to manage dollar spot than any other turfgrass disease, and >70% of fungicides applied on golf courses are for the management of three major turf diseases: dollar spot, brown patch, and anthracnose (Bonos 2006; Vargas 2005). When disease exceeds threshold levels and fungicide application is needed for control, the cost of the fungicide application often exceeds US$170/ha (Goodman and Burpee 1991; Rioux et al. 2014).

Clarireedia spp. have a broad host range and can infect all cultivated cool-season and warm-season turfgrasses. More than 40 plant hosts have been reported; however, the majority of host plants belong to the grass family Poaceae (Ostrander et al. 2014; Walsh et al. 1999). In addition to Poaceae, *Clarireedia* spp. have also been reported from the Cyperaceae (sedge), Caryophyllaceae (pink), Convolvulaceae (morning glory), and Leguminosae (pea) families (Walsh et al. 1999).

Symptoms of dollar spot vary depending on the turfgrass species and management practices. Under close mowing conditions of fine-textured grasses (e.g., bentgrass or bermudagrass), symptoms first appear as small, circular, straw-colored spots of blighted turfgrass about the size of a silver dollar (Fig. 1A and B), but when the mowing height is increased for coarser textured grasses (e.g., Kentucky bluegrass or ryegrass), the blighted spots are larger, irregularly shaped, straw-colored patches approximately 7 to 15 cm in diameter (Walsh et al. 1999). On individual blades of grass, early symptoms include chlorosis and water-soaking areas, and as the disease advances, the infected leaf tissues take on a straw-colored appearance of variable shape and size (Fig. 1C) (Walsh et al. 1999). Signs of infection with *Clarireedia* spp. may include white mycelium with a cobweb-like appearance (Fig. 1D) that may be seen early in the morning when dew is present.

Depending on the environmental conditions, the disease is most prevalent in the spring and fall, when days are warm and humid and heavy dew is present in the morning. The general disease cycle of dollar spot is illustrated in Figure 2. *Clarireedia* spp. overwinter or survive from one season to the next as mycelium or stromata in infected plant tissues, and these are an important source of primary inoculum for future disease development (Rioux et al. 2014; Walsh et al. 1999). Invasion of the leaf tissues by the pathogen occurs primarily via mycelial growth into cut leaf tips and natural openings (stomata), but direct penetration through the formation of appressoria also occurs (Allen et al. 2005). *Clarireedia* spp. do not produce spores; therefore, short-distance dissemination of the pathogen (i.e., plant-to-plant movement or movement to adjacent plants) occurs when the mycelium grows from diseased tissue onto healthy tissue in close proximity. Long-distance dissemination of the pathogen probably occurs by mechanical or physical movement of the pathogen or infected plant tissues by humans or other sources (Allen et al. 2005; Horvath et al. 2007; Walsh et al. 1999). Contaminated seeds are one possible source of long-distance dissemination. Viable and pathogenic *Clarireedia* spp. have been isolated from commercial seed lots of creeping bentgrass (Rioux et al. 2014).

Clarireedia spp. can survive over a wide range of temperatures, from 4 to 32°C, with the optimal temperature for infection between 15 and 27°C (Walsh et al. 1999). However, the optimum temperature necessary for infection may vary between biotypes present at different geographic locations (Smiley et al. 2005). Optimum temperature combined with high humidity (>85%) and prolonged periods of leaf

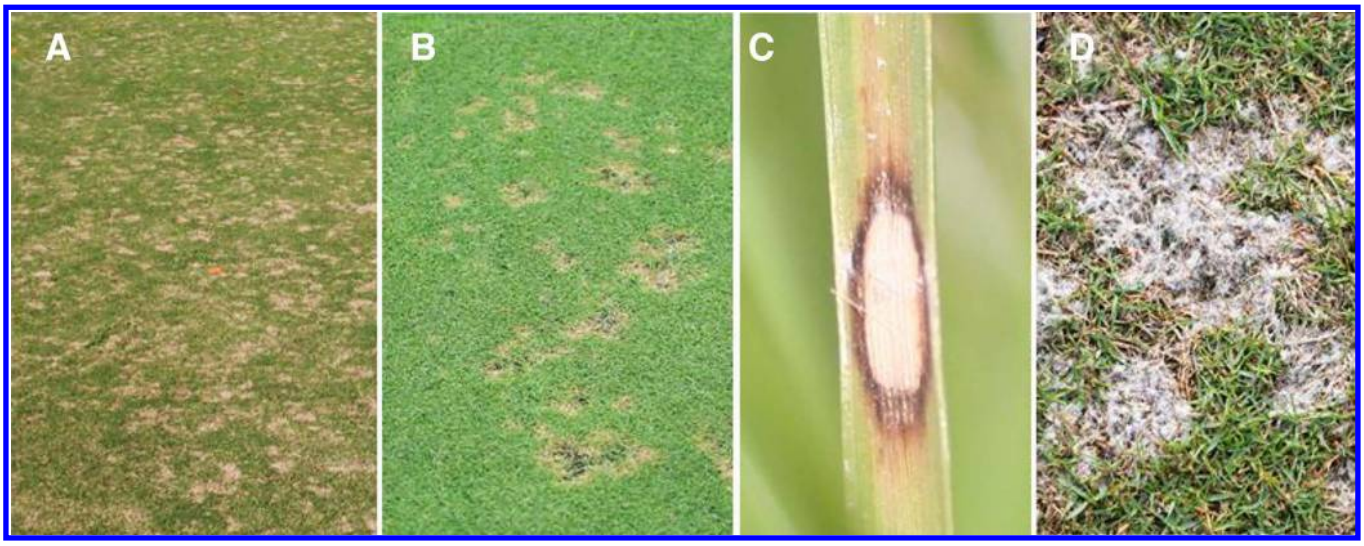

FIGURE 1

Symptoms and signs of dollar spot on turfgrass. Typical dollar spot symptoms on **A,** bermudagrass and **B,** bentgrass; **C,** lesion of dollar spot on zoysiagrass; **D,** sign of *Clarireedia* spp., white mycelium growth, on seashore paspalum.

wetness caused by rain or irrigation favor in planta growth of the fungus (Allen et al. 2005; Walsh et al. 1999). The amount and duration of leaf wetness are important factors in dollar spot epidemics (Ellram et al. 2007; Pigati et al. 2010; Walsh et al. 1999). In addition, dollar spot severity is also promoted by nutrients present in guttation fluids (Pigati et al. 2010). Guttation fluid may include amino acids, sugars, and carbohydrates, which can increase the ability of the pathogen to penetrate and grow in the host tissue (Pigati et al. 2010). Irrigation and availability of soil moisture also play an important role on the progress of a dollar spot epidemic. Couch and Bloom (1960) reported that disease development was significantly higher with irrigation practices that produced high soil moisture. However, McDonald et al. (2006) demonstrated that dollar spot severity increased when creeping bentgrass received deep and infrequent irrigation, and disease severity was negatively correlated with soil moisture. The effects of nitrogen fertilizer on dollar spot epidemics were also investigated (Allen et al. 2005; Townsend et al. 2021), and these studies indicate that high levels of nitrogen reduce dollar spot severity. Allen et al. (2005) proposed that grasses grown under nitrogen-starved conditions have greater amounts of senescent foliage, which could serve as a food source for the fungus promote the epidemic.

TAXONOMY AND NOMENCLATURE OF THE PATHOGEN

The taxonomy and nomenclature of the causal pathogen of dollar spot have long been in question and a subject of debate. Although the disease was first reported on turfgrass in 1927 (Monteith 1927), the first valid name for the dollar spot pathogen, *Sclerotinia homoeocarpa* F.T. Bennett, was provided by Bennett in 1937 (Bennett 1937). Bennett's classification and nomenclature of the dollar spot pathogen were later reviewed based on morphological and molecular characteristics, but no valid classification was made (Holst-Jensen et al. 1997; Powell 1999; Viji et al. 2004). Despite the advent of molecular technologies, global outbreaks, wide distribution, and the large economic impact of the disease (Smiley et al. 2005; Vargas 2005), the taxonomic classification of the causal agent remained unresolved until 2018. Based on three DNA markers (internal transcribed spacer [ITS] region, calmodulin, and DNA replication licensing factor Mcm7, Salgado-Salazar et al. (2018) placed the causal agent into a new genus, *Clarireedia*, as a member of the family *Rutstroemiaceae*. Most plant pathogens belonging to the *Rutstroemiaceae* family are saprotrophs, with a few exceptions of necrotrophic and biotrophic parasites (Salgado-Salazar et al. 2018; Zhao et al. 2016). Salgado-Salazar et al. (2018) described four species of the genus *Clarireedia*: *C. homoeocarpa*, *C. bennettii*, *C. jacksonii*, and *C. monteithiana*. Of these, *C. homoeocarpa* and *C. bennettii* are restricted to the United Kingdom, whereas *C. jacksonii* and *C. monteithiana* are globally distributed (Salgado-Salazar et al. 2018) and colocalized in adjacent turfgrass stands throughout the transition zone of the United States (Aynardi et al. 2019), particularly in the state of Georgia (Sapkota et al. 2020). These findings are consistent with the previous hypothesis by researchers that more than one fungal pathogen is causing dollar spot in turfgrass, based on variations observed in morphological and molecular characteristics of the pathogen (Liberti et al. 2012;

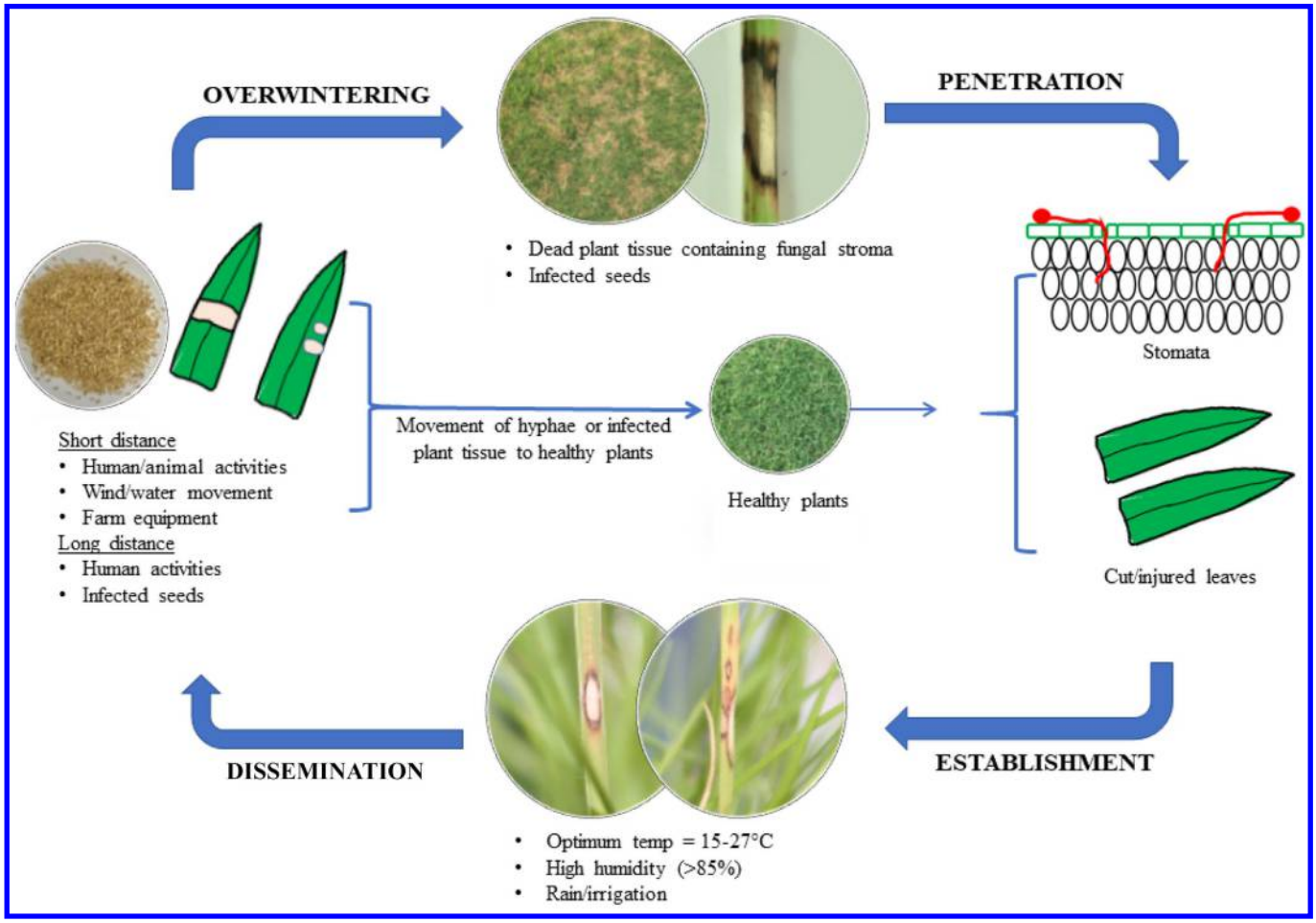

FIGURE 2
Disease cycle of *Clarireedia* spp. causing dollar spot on turfgrass (illustration by S. Sapkota).

Salgado-Salazar et al. 2018; Taylor 2010). *C. monteithiana* was shown to be more genetically closely related to *C. jacksonii* than to *C. homoeocarpa* and *C. bennettii*. Twenty-eight, 20, and eight species-specific single-nucleotide polymorphisms differentiating the four *Clarireedia* species were identified in the ITS, calmodulin, and Mcm7 sequences, respectively (Salgado-Salazar et al. 2018). Recently, Hu et al. (2019) reported new *Clarireedia* species, *C. paspali* and *C. aff paspali*, based on the multilocus phylogeny analysis (ITS, EF-1α, and Mcm7) from dollar spot samples collected from Hainan, Shanghai, and Jiangsu provinces of China on seashore paspalum. *C. paspali* was particularly differentiated from *C. aff paspali*, *C. jacksonii* and *C. monteithiana* by the presence of an intron at the 3′-end of the small subunit ribosomal ribonucleic acid region (Hu et al. 2019). Although significant progress has been made in the taxonomy and nomenclature of dollar spot pathogens, a more exhaustive sampling and use of next-generation sequencing technologies is needed to resolve dollar spot species ambiguities and classification.

DISEASE MANAGEMENT STRATEGIES

Several management strategies including cultural practices, use of fungicides, biological control, and host plant resistance have been used, singly or in combination, for the control of dollar spot in turfgrass. Below we summarize information on cultural, chemical, and biological controls of dollar spot. Dollar spot management based on host resistance will be discussed in the "Genetics and Mapping of Dollar Spot Resistance" section.

Cultural control. Cultural practices are important in controlling dollar spot and are often used by turfgrass managers as a component of integrated disease management (Delvalle et al. 2011). The removal of leaf wetness early in the morning with dew whips, mowing, or lightweight rollers can help decrease the incidence of dollar spot (Delvalle et al. 2011; Ellram et al. 2007; Giordano et al. 2012; Williams et al. 1996). Williams et al. (1996) reported that removal of morning leaf moisture in creeping bentgrass with mowers significantly reduced (≤81%) the severity of dollar spot. Studies have demonstrated that the frequency of leaf moisture removal is also important in dollar spot management. Daily dew removal was found to be more effective in controlling dollar spot than was dew removal on alternate days (Ellram et al. 2007). Collection and removal of dead plant tissues containing fungal stroma may help reduce the incidence of dollar spot because the pathogen overwinters on dead plant tissue (Walsh et al. 1999). Additionally, maintaining adequate soil fertility, particularly nitrogen (N), and optimizing irrigation systems to maintain adequate soil moisture were found effective in reducing dollar spot severity in turfgrass swards (Couch and Bloom 1960; McDonald et al. 2006). Williams et al. (1996) observed ≤57% reduction in dollar spot severity on 'Penncross' creeping bentgrass that was fertilized with 73.2 kg N/ha of granular urea (46-0-0) annually compared with a 0 kg N/ha control. Golembiewski and Danneberger (1998) and Townsend et al. (2021) also observed decreased dollar spot severity with higher rates of N fertilizer. Although the rate of N fertilizer had a substantial impact on the level of reduction in dollar spot, the source of N had minimal and inconsistent impacts on disease severity (Ryan et al. 2011; Townsend et al. 2021). The mechanisms underlying dollar spot response to N fertilization are unclear but probably include the buildup of competitive microbial populations, nitrogen-stimulated plant growth, and changes in foliar or soil pH that alter pathogen virulence or host plant resistance (Townsend et al. 2021). Cultural practices are an effective way of controlling dollar spot; however, haphazard use may limit their effectiveness. For example, potassium deficiencies increase disease, but adding potassium above the necessary levels provides no benefit (Johnson et al. 1987; Sartain 2002). Application of soluble silica may provide some degree of protection from dollar spot, but the protection is incomplete, and fungicide application is necessary for sufficient dollar spot control (Uriarte et al. 2004). Overall, dollar spot control should be a multiprong approach. Continued research on additional cultural practices and improvements to the ones we are currently using is needed to increase their effectiveness.

Chemical control. Although cultural practices have been found beneficial to control dollar spot, use of fungicides is typically necessary to achieve effective control when disease pressure is high. Methyl benzimidazole carbamate, demethylation inhibitors, dicarboximides, succinate dehydrogenase inhibitors, chloronitriles, and quinone outside inhibitors are common classes of fungicides that are effective in controlling dollar spot (Allen et al. 2005; Clarke et al. 2020; Latin 2011). Proper timing of fungicide applications is critical for dollar spot management, and weather-based models have been developed and validated on turfgrass to predict the onset of dollar spot epidemics and advise managers when fungicide applications are needed. Ryan et al. (2012) developed a growing degree day model that uses a base temperature of 15°C, which can accurately predict the onset of the initial dollar spot epidemic in creeping bentgrass, but this model is not applicable to subsequent epidemics within the growing season. More recently, Smith et al. (2018) developed and validated a weather-based dollar spot warning system that requires the measurement of mean daily air temperature and relative humidity and can accurately predict the onset of a dollar spot epidemic and inform fungicide applications. This model can reduce fungicide usage by ≤30%. Currently available warning systems can be used as an important tool in effective control of dollar spot; however, further refinements, particularly using more diverse and multiple-year data, are warranted.

The repeated use of fungicides has led to the emergence of fungicide resistance to demethylation-inhibiting (DMI), benzimidazole, and succinate dehydrogenase inhibitor (SDHI) fungicides in *Clarireedia* spp. populations (Bishop et al. 2008; Jo et al. 2008a; Ok et al. 2011; Popko et al. 2018). Additionally, several isolates of the dollar spot pathogen have been shown to exhibit multiple resistance (i.e., resistance to more than one fungicide belonging to different classes) and cross-resistance (Jo et al. 2006; Ok et al. 2011; Stephens and Kaminski 2019). Nevertheless, Hsiang et al. (1997) used field populations of *Clarireedia* spp. collected in 1994, before DMI fungicides were registered for turfgrass disease control in Canada, and observed a wide range of sensitivity to the DMI fungicides propiconazole, myclobutanil, fenarimol, and tebuconazole. They also reported that cross-resistance to DMI fungicide may not be as strong as previously thought. In another study, Hsiang et al. (2007) observed a shift toward reduced DMI fungicide sensitivity with significantly greater half maximal effective concentration values, indicating that fungicide resistance in *Clarireedia* spp. populations is developing over time. Limited studies have been carried out to elucidate the genetic factors governing fungicide resistance in *Clarireedia* spp. Popko et al. (2018) observed differential resistance to SDHI fungicides by using field isolates collected from two separate continents and also reported that the presence of multiple target gene mutations in *Clarireedia* spp. is causing the differential cross-resistance. A study conducted by Hulvey et al. (2012) found that overexpression of two genes, *ShCYP51B* and *ShatrD*, in the dollar spot pathogen is responsible for reduced DMI fungicide sensitivity. Additionally, Sang et al. (2017) found that nonsynonymous polymorphisms in codon 366 (isoleucine to asparagine) in histidine kinase gene (*Shos1*) and overexpression of *ShPDR1* led to dicarboximide resistance in *Clarireedia* spp. isolates.

Ferrous sulfate has been proven effective to control dollar spot in turfgrass (McCall et al. 2017; Shelton et al. 2021) and can be an alternative to DMI and SDHI fungicides. McCall et al. (2017) reported that applications of ferrous sulfate (48.8 kg/ha) on a 14-day interval reduced dollar spot severity by >50% throughout a season (May to September) without affecting turfgrass quality. However, Ervin et al. (2017) and Mattox et al. (2017) reported that

the overall quality of creeping bentgrass was reduced when it was treated with ferrous sulfate. More recently, Shelton et al. (2021) reported a nonlinear relationship between the rate of ferrous sulfate application and dollar spot development where only 26.4 kg/ha of ferrous sulfate is needed to suppress dollar spot by 50%. More research is needed to determine the optimum rate of ferrous sulfate application to control dollar spot without compromising turf quality.

Biological control. Several studies have investigated biological agents as controls for dollar spot on turfgrass. Primarily, antagonistic microorganisms, hypovirulent strains of *Clarireedia* spp., and biological and oil-based fungicides have been shown to hold promise as potential controls for dollar spot (Koch et al. 2020; Walsh et al. 1999; Zhou and Boland 1998). In both field and greenhouse trials, top-dressing creeping bentgrass with a sand–cornmeal mixture infested with *Fusarium heterosporum* (isolate pa 7) (Goodman and Burpee 1991) and *Enterobacter cloacae* strain EcCT-501 (Nelson and Craft 1991) suppressed dollar spot by 25 to 90% and 63%, respectively. In a growth chamber study using creeping bentgrass infested with dollar spot, the disease was reduced by *Trichoderma harzianum* strain 1295-22 by ≤71% in field trials conducted over 4 years (Lo et al. 1996). Bacterial endophytes from *Zea* spp. identified as *Burkholderia gladioli* also suppressed dollar spot in creeping bentgrass in greenhouse trials (Shehata et al. 2016). On Kentucky bluegrass (*Poa pratensis*) infested with dollar spot, chlorophyll loss was reduced when leaves were inoculated with *Streptomyces diastaticus* (S32), *S. glabus* (S35), *S. hygroscopicus* (S13) (Hodges et al. 1993), *Pseudomonas fluorescens* (strains PSD-4, PSD-5, and PSD-6), and *P. lindbergii* strain PSD-42 (Hodges et al. 1994). Investigation of *P. fluorescens* strain Pf-5 showed that it reduced mycelial growth of the pathogen and also reduced dollar spot incidence in turfgrass (Rodriguez and Pfender 1997). *P. fluorescens* is known to produce antifungal metabolites such as pyoluteorin, pyrrolnitrin, and 2,4-diacetylphloroglucinol. Mutants of Pf-5 deficient in pyrrolnitrin did not reduce dollar spot on infested grass clippings, whereas Pf-5 did, and a pyoluteorin-deficient mutant had an intermediate reduction of disease. Another species of *Pseudomonas*, *P. aureofaciens* Tx-1(ATCC 55670), exhibited antifungal properties from an identified active component phenazine-1 carboxylic acid (Powell et al. 2000). Phenazine-1 carboxylic acid showed disease suppression similar to that of the commercial fungicides triadimefon and chlorothalonil on creeping bentgrass infested with dollar spot (Powell et al. 2000). Similarly, Clarke et al. (2020) listed *Bacillus licheniformis* (trade name EcoGuard) and *B. subtilis*, strain QST 713 (trade name Rhapsody) as potential biological control agents for dollar spot. However, Koch et al. (2020) evaluated six commercially available biological fungicides including *S. lydicus* (Actinovate AG), *B. amyloliquefaciens* (Double Nickel LC), *B. firmus* (Nortica), *B. subtilis* (Rhapsody), *B. subtilis* (Serenade Opti), and *P. chloroaphis* (Zio) and two oil-based fungicides, mineral oil (Civitas) and tea tree oil (Timorex Gold) for dollar spot control on creeping bentgrass, and none of these products provided effective full-season control comparable to the fungicide boscalid. Only the mineral oil-based fungicide was able to provide dollar spot control similar to boscalid on nine out of 12 assessments over the 2-year evaluation.

In addition to antagonistic microorganisms, hypovirulent strains of *Clarireedia* spp. have been used to suppress dollar spot. Hypovirulence, the reduced ability of the pathogen to infect susceptible host tissue, is often associated with the presence of double-stranded RNA and is transmissible between infected and healthy pathogen isolates (Deng et al. 2003; Walsh et al. 1999). Hypovirulent isolates often grow slowly on media, develop thin colonies with unusual colony margins, and fail to produce typical black stroma (Zhou and Boland 1997). In growth chamber and field environments on creeping bentgrass, applications of hypovirulent isolates (Sh12B, Sh09B, and Sh08D) resulted in 3.4 to 30.4% disease severity compared with 80.2 to 90.2% disease severity when infested with virulent strains (Sh48B or Sh14D) (Zhou and Boland 1998). The isolate Sh12B applied as a mycelial suspension was able to significantly suppress the disease in creeping bentgrass even 1 year after inoculation. A single application of isolate Sh12B, containing positive-strand RNA virus *Ophiostoma mitovirus 3a*, showed disease suppression as effective as four applications of fungicide (Boland 2004). Kabbage et al. (2020) reported that poacic acid, a secondary metabolite produced by many grass species (Poaceae family), inhibits the growth of *C. jacksonii* by 93% and suppresses the development of dollar spot in the field by 54 and 67% when applied at 61.76 and 30.88 ml/100 m^2, respectively, relative to the nontreated control. Recently, Coelho et al. (2021) reported that organic composts enriched with nonpathogenic soilborne fungus *Trichoderma atroviride* are beneficial in controlling turfgrass diseases including dollar spot.

GENETIC DIVERSITY, GENOMICS, AND HOST–PATHOGEN INTERACTIONS

Genetic diversity in *Clarireedia* spp. populations has been of great interest in the turfgrass scientific community and was determined mainly in terms of vegetative compatibility groups (VCGs), molecular markers, and mating locus. VCGs have been widely used in *Clarireedia* spp. to investigate the genetic diversity (Deng et al. 2002; DeVries et al. 2008; Mitkowski and Colucci 2006; Powell and Vargas 2001; Viji et al. 2004), and four to 20 VCGs have been reported. Powell and Vargas (2001) conducted the most extensive genetic diversity study by using >1,300 *Clarireedia* spp. isolates. However, these isolates were collected from a small geographic location (i.e., Michigan, Illinois, and Wisconsin) and lacked genetic diversity, with only six VCGs reported. A more comprehensive genetic diversity study with the most geographically diverse collection of *Clarireedia* spp. isolates was conducted by Viji et al. (2004). In this study, 67 isolates were collected from the United States and Canada between 1972 and 2001, and a total of 11 VCGs were reported. Although results from these studies reported varying numbers of VCGs, the genetic diversity within the *Clarireedia* spp. population was reported to be minimal. Similarly, several studies based on nuclear markers have shown low genetic diversity among *Clarireedia* spp. isolates (DeVries et al. 2008; Iriarte et al. 2003; Jo et al. 2008a; Powell and Vargas 2001; Ruiz et al. 2006). The low level of genetic diversity among isolates of *Clarireedia* spp. is probably caused by the presence of clonal populations that lack an identified sexual cycle (no fertile apothecia) (DeVries et al. 2008; Powell and Vargas 2001; Viji et al. 2004). Similarly, the mating type locus has also been investigated, and findings indicated heterothallic control of the mating type and potential for the occurrence of sexual reproduction in nature (Liberti et al. 2012; Putman et al. 2015). Low levels of linkage disequilibrium were observed in several dollar spot populations collected from Ontario, Canada (Hsiang and Mahuku 1999), indicating that these populations are undergoing random mating. In addition, heterokaryosis is an important phenomenon for increasing genetic variability in many fungal pathogens that lack sexual recombination. Heterokaryosis in *Clarireedia* spp. was first reported by Jo et al. (2008b), and since then several reports have been published with evidence of heterokaryosis in *Clarireedia* spp. and its putative role in increasing genetic variability (Kessler et al. 2018; Putman et al. 2015). More exhaustive genetic and genomic investigations are needed to clarify the contributions of the sexual and parasexual reproductions in *Clarireedia* spp. genetic variability in nature. Overall, genotyping of dollar spot isolates collected from different geographic locations and hosts revealed that the population structure of the pathogen correlated with the host species rather than the geographic origin of the isolate (DeVries et al. 2008; Putman 2013; Salgado-Salazar et al. 2018; Taylor 2010; Viji et al. 2004). Pathogen isolates from cool-season

(C3) and warm-season (C4) grass hosts were differentiated into two distinct clades and were classified as *C. jacksonii* and *C. monteithiana*, respectively, in the United States (Salgado-Salazar et al. 2018). A similar result was reported by Aynardi et al. (2019) and Sapkota et al. (2020), who identified dollar spot isolates collected from C3 and C4 grass species as *C. jacksonii* and *C. monteithiana*, respectively. However, cross-inoculation experiments demonstrated that both *Clarireedia* species are capable of cross-infecting grasses belonging to both C3 and C4 photosynthesis pathways (Fig. 3; Aynardi et al. 2019; Sapkota et al. 2020). Aynardi et al. (2019) also observed higher disease severity of *C. jacksonii* isolates compared with *C. monteithiana* isolates, when these pathogens were evaluated on both C3 and C4 turfgrasses. In addition, in contrast to previous studies, Hu et al. (2019) reported that *C. jacksonii* isolates are not restricted to cool-season grasses and were isolated from the warm-season grass *Paspalum vaginatum* in China.

Whole genome sequencing and comparative genomics are powerful approaches to reveal pathogen genetic diversity, pathogen population structure, and evolution. However, a complete genome sequence of *Clarireedia* species is lacking, and only draft genome sequences of 10 isolates causing dollar spot in turfgrass have been reported (https://www.ncbi.nlm.nih.gov/genome/). The main genome features of these 10 *Clarireedia* spp. sequenced isolates are listed in Table 1. Differences in genome size, ranging from 29.72 to 48.70 Mb, were observed among these isolates. Green et al. (2016) sequenced at scaffold level two isolates, HRI11 and HRS10, sampled from *Agrostis stolonifera* in 2009, which are fungicide-resistant and sensitive strains, respectively (Table 1). The draft genomes for the two isolates were aligned against *Clarireedia* spp. reference ITS and Mcm7 sequences available from GenBank, and these two strains were classified as *C. jacksonii* with 99 to 100% identity. Although sampled the same year at the same location, these two *C. jacksonii* isolates showed an average identity at the DNA level of only 79% across the genome (B. Bahri, *unpublished data*), suggesting a potentially high genetic diversity within this species. Genome sequence data are available for eight isolates (Table 1) including four *C. jacksonii* (LWC-10, MB-01, SH44, and SE16F4), two *C. monteithiana* (DRR09 and RB-19), and two unknown species (CPB17 and LT30) (Crouch et al. 2021; Salgado-Salazar et al. 2018). Based on the sequence alignment against *Clarireedia* spp. reference ITS and Mcm7 sequences, it was determined that the unknown isolate CPB17 is *C. jacksonii* with 93.7 and 91.7% identity, respectively. Similarly, LT30 sampled from *A. stolonifera* was also classified as *C. jacksonii* based on sequence alignment against *Clarireedia* spp. reference ITS and Mcm7 sequences with 100 and 99.8% identity, respectively (B. Bahri, *unpublished data*). Crouch et al. (2021) also investigated the number of predicted gene models in each of the *Clarireedia* spp. isolates sequenced and found that it ranged from 10,821 to 11,134 genes, with the exception of DRR09. The *C. monteithiana* isolate DRR09 contains 16,244 predicted gene models, higher than other sequenced isolates (Table 1).

FIGURE 3

Cross-infection of **A,** *Clarireedia jacksonii* on zoysiagrass (C4 turfgrass), and **B,** *C. monteithiana* on bentgrass (C3 turfgrass). The plant materials were artificially inoculated at the University of Georgia Griffin Campus greenhouse as described by Sapkota et al. (2020).

The interaction between *Clarireedia* spp. and turfgrass species is a critical part of our understanding of how the pathogens infect and how to control the spread of the disease. In 2008, oxalic acid, a compound previously identified as an important pathogenicity factor in the closely related dicot pathogen *Sclerotinia sclerotiorum* (Bolton et al. 2006), was detected in pure cultures of *Clarireedia* spp. (Beaulieu 2008; Venu et al. 2009). Since then, few studies have been published on the dollar spot–turfgrass pathosystem, with most focusing on the role of oxalic acid during infection. These studies showed an increase in oxalic acid content of *Clarireedia* spp. infected host tissue (Orshinsky et al. 2012a; Rioux et al. 2021); upregulation of germin-type oxalate oxidases, plant enzymes unique to Gramineae capable of degrading oxalic acid, in creeping bentgrass infected with *Clarireedia* spp. (Orshinsky et al. 2012b); and greater activity of these defense-related enzymes in a creeping bentgrass cultivar moderately resistant to dollar spot than in a susceptible one (DaRoche and Hammerschmidt 2004). In addition, whole plant inoculation assays showed that oxalic acid content in plant tissue correlates with symptom development (Rioux 2014). Microscopic and macroscopic observations of *C. jacksonii*-infected tissues showed similar infection progression in several monocots tested (creeping bentgrass, wheat, barley, rice, and *Brachypodium distachyon*), with extensive colonization of host tissue by 12 to 24 h after inoculation. However, oxalic acid production was increased with inoculation only in creeping bentgrass, wheat, and barley but not in rice and *Brachypodium distachyon*, plant species known for their high endogenous oxalate (mineral salts of oxalic acid) content (Rioux et al. 2021). Townsend et al. (2020) also suggested that oxalic acid production by *C. jacksonii* depends on the host tissue composition and is influenced by the ambient pH of the foliar environment during infection and symptom development. Oxalic acid production was 89 to 190% higher in potato dextrose broth at pH 7 than at pH 4. Oxalic acid production was also shown to significantly increase in potato dextrose broth amended with creeping bentgrass tissue and xylan, a component of the host cell wall (Townsend et al. 2020). The Townsend et al. (2020) study also suggested differences in pathogenesis between *C. jacksonii* and *S. sclerotiorum*, reinforcing the importance of performing more genomic and proteomic investigations to clarify the infection process of *Clarireedia* species. Oxalic acid might have a lesser role in *Clarireedia* pathogenicity than we think. In fact, Orshinsky et al. (2012b) performed RNA sequencing analysis and pointed out several enzymes that could play an important role in the pathogenesis of *Clarireedia* species. *Clarireedia* spp. transcripts in the dollar spot interacted creeping bentgrass library were enriched with glycosyl hydrolase enzymes such as xylanases and with serine proteases (Orshinsky et al. 2012b). These enzymes were reported as pathogenicity factors in several plant pathogenic fungi and supported the wide host range of *Clarireedia* spp. (Li et al. 2010; Rowe and Kliebenstein 2007).

GENETICS AND MAPPING OF DOLLAR SPOT RESISTANCE

Use of resistant cultivars is a promising method to control dollar spot, and cultivars with partial resistance have been reported for many common turfgrass species (Benda et al. 2017; Koch and Kerns 2012; Steketee et al. 2017). However, cultivars with

complete resistance or immunity to dollar spot are lacking. Three creeping bentgrass clones, Penncross-2, L93-10, and 7335-2, were reported as resistant when evaluated under field conditions against three dollar spot isolates (H1, H2, and H3) (Bonos 2006; Bonos et al. 2003). Williams (2005) evaluated genotypes of bahiagrass (*Paspalum notatum*) for resistance to dollar spot and found that two tetraploid cultivars, 'Argentine' and 'Tifton 7', are less susceptible to the disease, based on 2 years of screening data. Similarly, evaluation of 79 clones of bentgrass obtained from 10 cultivars against *Clarireedia* spp. isolates representing 10 vegetative compatibility groups detected significant differences between bentgrass cultivars in their response to dollar spot. Two of eight creeping bentgrass cultivars, 'Declaration' and 'Memorial', exhibited partial resistance when evaluated for dollar spot resistance over a 3-year period (Koch and Kerns 2012). Raymer et al. (2008) and Steketee et al. (2017) evaluated seashore paspalum germplasm for their reaction to dollar spot and reported some partially resistant genotypes (i.e., PI 647907, PI 647921, and SeaIsle 2000), which could be used in the breeding program to develop cultivars with improved dollar spot resistance. Flor et al. (2013) and Benda et al. (2017) screened seashore paspalum cultivars for their reaction to dollar spot and identified two genotypes, UF19-18 and SeaDwarf, with less severe dollar spot symptoms. However, the results between the two studies were inconsistent. For example, genotype BA511-2 was identified as resistant to an isolate sampled from seashore paspalum (UF0421) under greenhouse conditions in the Flor et al. (2013) study but was one of the most susceptible in the Benda et al. (2017) study. The difference in phenotypic reaction for some of the genotypes, including BA511-2, between these two studies indicates that better screening methods that generate reliable and repeatable data will be essential to obtain reliable sources of resistance and to effectively breed for improved resistance to this pathogen. Evaluation of 25 creeping bentgrass cultivars across five states in the central United States determined that two cultivars, 'Kingpin' and 'Memorial', had the least dollar spot injury across environments (Thompson et al. 2019). Information on the level of resistance or susceptibility of specific turfgrass species can be obtained from the National Turfgrass Evaluation Program (www.ntep.org).

Genetic mechanisms of dollar spot resistance in turfgrass are not well characterized, and only a few studies have been conducted. Studies on creeping bentgrass demonstrated that dollar spot resistance is quantitatively inherited (Bonos 2006, 2011; Bonos et al. 2003; Chakraborty et al. 2006b). Based on classic genetic analysis, Bonos et al. (2003) reported that two to five genetic factors or genes, depending on the cross, were responsible for dollar spot resistance in creeping bentgrass. Similarly, based on the distribution of phenotypic data of 90 seashore paspalum accessions evaluated for reaction to dollar spot, Steketee et al. (2017) indicated that dollar spot resistance in seashore paspalum is probably quantitative. Using five seashore paspalum cultivars with varying levels of dollar spot resistance and five *Clarireedia* spp. isolates sampled from warm- and cool-season turfgrass species, Steketee et al. (2016) observed no significant interaction between genotypes and isolates, indicating that dollar spot resistance in seashore paspalum is probably not isolate-specific. The heritability of dollar spot resistance in creeping bentgrass and seashore paspalum varied from low (0.23) to high (0.90) depending on the resistant lines used (Bonos 2006; Bonos et al. 2003; Chakraborty et al. 2006b; Flor et al. 2013).

The development of genetic linkage maps and subsequent QTL mapping has been the most common and widely used approach in molecular breeding to identify genomic regions associated with the trait of interest. However, limited efforts have been directed to linkage map construction in turfgrass species and mapping genes or QTLs for dollar spot resistance. The general scheme of QTL mapping and marker-assisted selection (MAS) for dollar spot resistance is illustrated in Figure 4. Chakraborty et al. (2005) constructed the first linkage map in allotetraploid creeping bentgrass by using a mapping population derived from the cross between two highly heterozygous parental clones, 372 and 549, selected from 700 clones.

TABLE 1
***Clarireedia* spp. isolates that have been sequenced and assembled at scaffold level and their genomic features**

				Features of the genome							
Clarireedia spp.[a]	Host of origin	Region of origin	Year of collection	Genome size (Mb)	GC content (%)	Scaffolds	Scaffold N50 (bp)	Predicted genes	Sequencing method[b]	GenBank accession no.	Reference
C. jacksonii (HRI11)	*Agrostis stolonifera*	Massachusetts, USA	2009	43.35	43.83	257	709,078	–	Illumina and PacBio	LNKV00000000	Green et al. 2016
C. jacksonii (HRS10)	*Agrostis stolonifera*	Massachusetts, USA	2009	42.26	43.35	231	600,417	–	Illumina and PacBio	LNGN00000000	Green et al. 2016
C. jacksonii (CPB17)	*Festuca rubra*	United Kingdom	2008	36.40	46.6	3,875	20,651	11,134	Illumina (41×)	LLKJ00000000	Crouch et al. 2021
C. jacksonii (SE16F4)	*Festuca rubra*	United Kingdom	2008	36.00	46.1	4,789	15,633	11,035	Illumina (38×)	LLKF00000000	Crouch et al. 2021
C. jacksonii (LT30)	*Agrostis stolonifera*	Massachusetts, USA	2009	29.72	44.6	31,623	–	–	–	AKKO00000000	NCBI
C. monteithiana (DRR09)	*Paspalum vaginatum*	Dominican Republic	2008	48.70	44.8	15,133	8,758	16,244	Illumina (109×)	LLKI00000000	Crouch et al. 2021
C. monteithiana (RB-19)	*Cynodon dactylon*	Mississippi, USA	2008	36.10	44.7	3,610	20,763	10,821	Illumina (33×)	LLKG00000000	Crouch et al. 2021
C. jacksonii (LWC-10)	*Agrostis stolonifera*	North Carolina, USA	2003	37.20	41.6	3,606	25,161	11,089	Illumina (58×)	LLKH00000000	Crouch et al. 2021
C. jacksonii (MB-01)	*Agrostis stolonifera*	Ohio, USA	2001	39.50	39.7	1,637	168,655	10,979	Illumina (70×)	LLKD00000000	Crouch et al. 2021
C. jacksonii (SH44)	*Agrostis stolonifera*	Canada	2000	35.90	45.1	3,468	17,322	10,975	Illumina (41×)	LLKE00000000	Crouch et al. 2021

[a] The species names for isolates HRI11, HRS10, and LT30 were identified according to Salgado-Salazar et al. (2018), by aligning the draft genomes of each isolate against *Clarireedia* spp. reference ITS/CaM sequences available at the GenBank. The features of *Clarireedia* spp. isolate LT30 were obtained from the NCBI website (https://www.ncbi.nlm.nih.gov/genome/).
[b] The average coverage of the sequencing method for each assembled genome is presented in parentheses.

The map was constructed with 424 loci distributed on 14 linkage groups and covered a total genetic distance of 1,110 cM. Honig et al. (2014) constructed another linkage map of creeping bentgrass by using a mapping population derived from two heterozygous bentgrass parental clones, 7418-3 and L93-10. As expected, 14 linkage groups were generated for each parent, covering a total genetic distance of 1,424 and 1,374 cM for the 7418-3 and L93-10 parental maps, respectively. Rotter et al. (2009) constructed the first linkage map for colonial bentgrass (*Agrostis capillaris* L.) by using a backcross population derived from creeping bentgrass and colonial

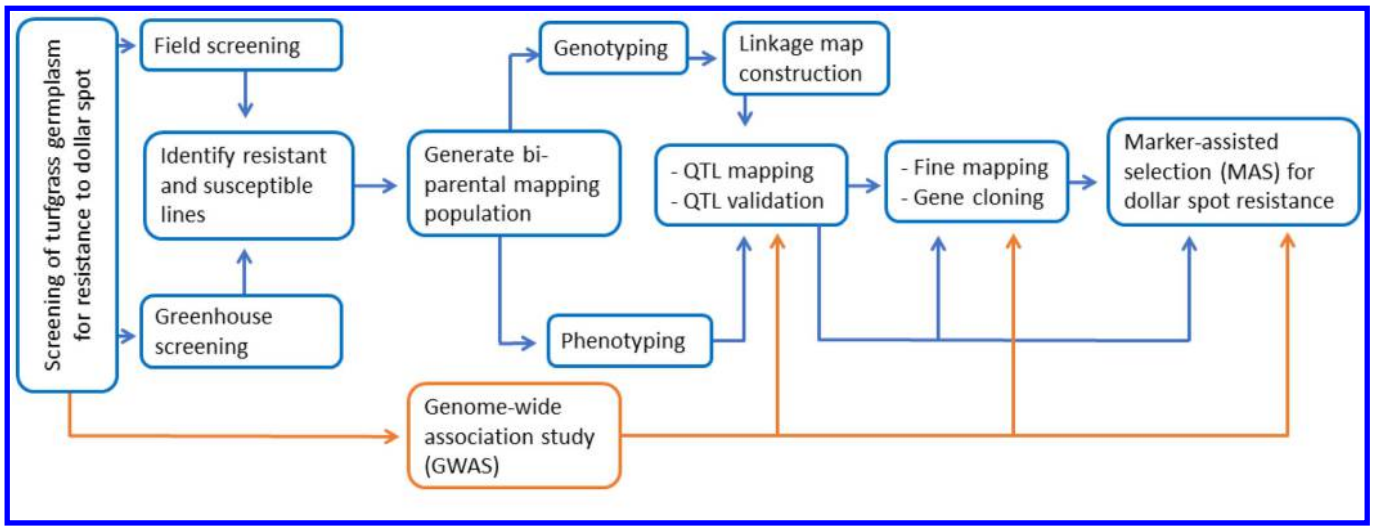

FIGURE 4
Schematic flow diagram illustrating quantitative trait locus (QTL) mapping and marker-assisted selection for resistance to dollar spot in turfgrass.

TABLE 2
Summary of linkage maps developed in turfgrass species and quantitative trait locus (QTL) analysis for dollar spot resistance

Turfgrass species	Population	Features of linkage map					QTLs for dollar spot resistance[f]	References
		No. of markers[a]	Marker types[b]	LGs[c]	Length (cM)[d]	Range (cM)[e]		
Zoysia spp.	Interspecific hybrid of zoysiagrass	115	RFLP	22	1,506.3	12.5–141.3	–	Yaneshita et al. 1999
Paspalum notatum (2n)	$Q4084_{10}/Tift_9$	112	RFLP, AFLP, RAPD	10	991	–	–	Ortiz et al. 2001
Lolium perenne	155 F1 progeny (p150/112)	172	SSR, AFLP, RFLP	7	814	–	–	Jones et al. 2002
Zoysia japonica	78 selfed progeny obtained from a clone "F02"	364	AFLP	26	932.5	–	–	Cai et al. 2004
Agrostis stolonifera	106 full-sib mapping population (549/372)	578	AFLP, RFLP, RAPD	14	1,125	44–114	Major QTL on LG 7.1 (14.1–36.0%) Minor QTL on LGs 2.1, 3.2, 4.1, 4.2, 6.2, and 7.2 (5.9–15.0%)	Chakraborty et al. 2006a
Agrostis capillaris	93 backcross population (colonial bentgrass/ creeping bentgrass)	322	AFLP, gene-based markers	14	1,156	–	–	Rotter et al. 2009
Agrostis stolonifera	181 pseudo F2 population (7418-3/L93-10)	385 (7418-3) 328 (L93-10)	SSR, AFLP, CISP, ILP	14	1,424 (7418-3) 1,374 (L93-10)	62–169	Eight QTLs on LGs 1.1, 4.1, 5.1, 5.2, 6.2, and 7.2 (8.5–16.2%)	Honig et al. 2014
Cynodon dactylon	110 F1 progeny (T89/ T574)	291 (T89) 125 (T574)	SSR, RFLP	–	–	–	–	Khanal et al. 2017
Paspalum vaginatum	226 F1 progeny (509022/ HI33)	4,078	SNP	10	–	–	–	Qi et al. 2019

[a] Total number of markers used to construct the linkage map.
[b] AFLP, amplified fragment length polymorphism; CISP, conserved intron scanning primer; ILP, intron length polymorphism; RAPD, random amplified polymorphic DNA; RFLP, restriction-fragment length polymorphism; SNP, single-nucleotide polymorphism; SSR, simple sequence repeat.
[c] Number of linkage groups (LGs).
[d] Total length (cM) of the linkage map.
[e] The range of genetic distance covered by LGs in the map.
[f] Only a few of the generated linkage maps were subsequently used for the identification of QTLs for dollar spot resistance. The numeric value in parentheses indicates the phenotypic variation explained by the QTL.

bentgrass. Similarly, linkage maps have been constructed for zoysiagrass (Cai et al. 2004; Yaneshita et al. 1999), perennial ryegrass (Jones et al. 2002), bermudagrass (Khanal et al. 2017), diploid *Paspalum notatum* (Ortiz et al. 2001), and seashore paspalum (Qi et al. 2019), which can be used for genetic studies (Table 2).

Using some of these linkage maps, QTL mapping has been conducted for resistance to dollar spot. Using the linkage map earlier developed by Chakraborty et al. (2005) and by adding more polymorphic markers to the map, Chakraborty et al. (2006b) reported a large-effect QTL for dollar spot resistance in creeping bentgrass on linkage group 7.1 with a logarithm of odds (LOD) value that ranged from 3.4 to 8.6 and explained ≤36% of the phenotypic variation (Table 2). The randomly amplified polymorphic DNA (RAPD) marker, 3.AW10.650, was found to be significantly associated with the QTL and was contributed by creeping bentgrass line 372. Additionally, several small effect QTLs were also reported for dollar spot resistance. Because the RAPD marker 3.AW10.650 was difficult to use in MAS, it was converted into a more user-friendly sequence characterized amplified region marker in a subsequent study facilitating its use in MAS for developing elite creeping bentgrass cultivars with improved dollar spot resistance (Chakraborty et al. 2014). Similarly, Honig et al. (2014) reported eight QTLs on linkage groups 1.1, 4.1, 5.1, 5.2, 6.2, and 7.2 for dollar spot resistance in creeping bentgrass (Table 2). The QTLs were contributed by both parents, 7418-3 and L93-10, and explained ≤16.2% of phenotypic variation. Using a backcross mapping population and linkage map derived from colonial bentgrass and creeping bentgrass, Rotter et al. (2009) conducted QTL mapping for dollar spot resistance. Although dollar spot–resistant individuals were present in the mapping population, no QTLs for dollar spot resistance were detected. Rotter et al. (2012) used the same population but an alternative approach to identify chromosomal regions associated with dollar spot resistance in colonial bentgrass. The authors selected a set of colonial bentgrass markers and screened all dollar spot–resistant lines present in the population. The result demonstrated that clusters of markers present on linkage groups $2A_1$ and $3A_1$ were present in all resistant lines, indicating that these chromosomal regions probably contain genes for dollar spot resistance in colonial bentgrass.

FUTURE RESEARCH PERSPECTIVES

Dollar spot is one of the most economically important diseases of turfgrass worldwide. Several management strategies including cultural, biological, chemical, and host resistance have been used, solely or in combination, to control dollar spot. However, when environmental conditions are favorable and disease pressure is high, fungicides are needed to control the disease. Use of host resistance is an important approach to control this disease; however, germplasm with high levels of dollar spot resistance is currently lacking in most turfgrass species. Integrated disease management is the most effective means of controlling dollar spot, and genetic resistance and fungicides are important tools in an integrated dollar spot management program. We believe that future research efforts aiming to effectively manage this disease problem should focus on the following areas.

Among the five species of *Clarireedia* causing dollar spot, *C. jacksonii* and *C. monteithiana* are globally distributed and predominantly infect C3 (cool-season) and C4 (warm-season) hosts, respectively in the United States. Although cross-inoculation experiments have demonstrated that both species are able to infect and cause disease on both C3 and C4 hosts (Aynardi et al. 2019; Sapkota et al. 2020), more host–pathogen interaction research is needed to confirm this C3 and C4 host preference of *C. jacksonii* and *C. monteithiana* and to exploit it in resistance breeding. Identifying the genetic components that confer an underlying background of host preference on C3 versus C4 turfgrass could provide a valuable source of dollar spot resistance. Several genes that confer resistance to nonadapted pathogens in one species have been successfully transferred to other host species to provide resistance to virulent isolates of the same pathogen. Nonhost resistance–linked genes from *Arabidopsis* were transferred to soybean for resistance to soybean rust (Langenbach et al. 2016), and maize *Rxo1* NLR genes were transferred to rice for bacterial streak resistance (Zhao et al. 2005). Similarly, Salgado-Salazar et al. (2018) reported that two other species, *C. homoeocarpa* and *C. bennettii*, are restricted to the United Kingdom and occur primarily on *Festuca rubra*, a C3 grass host. Therefore, more research is needed to determine whether *C. homoeocarpa* and *C. bennettii* have a host preference.

Phenotyping is a major constraint for the development of turfgrass species with improved dollar spot resistance; therefore, development of rapid and accurate protocols to screen turfgrass germplasm for resistance to dollar spot and pathogen virulence is needed. Artificial inoculation with infected seeds or grain and subsequent visual ratings (severity, incidence, scoring on a 1 to 9 rating scale) or digital image analysis is the most documented form of screening turfgrass germplasm for dollar spot resistance under field conditions (Bonos 2006, 2011; Honig et al. 2014; Steketee et al. 2017). Although this screening method can be effective, it takes a lot of time, space, and resources. Therefore, alternative methods, such as a quick and accurate detached leaf assays (DLAs), are needed for developing turfgrass germplasm with increased dollar spot resistance. Previously, Zhou and Boland (1997) and Steketee (2014) have used DLAs to phenotype the turfgrass germplasm against dollar spot isolates. However, results obtained from DLAs were not consistent with the field screening (Steketee 2014). Therefore, we need further research and refinement to be able to use it confidently in breeding programs.

Molecular techniques have become an effective method for accurate and early diagnosis of plant pathogenic fungi (Aslam et al. 2017). Groben et al. (2020) developed a quantitative real-time PCR assay to detect and quantify *Clarireedia* spp. from field samples in 3 h. However, the assay was not able to differentiate between *Clarireedia* species. Recently, Stackhouse et al. (2021) developed a codominant cleaved amplified polymorphic sequence assay and were able to characterize *Clarireedia* spp. to the species level, but this assay differentiates only two species, *C. monteithiana* and *C. jacksonii*. Therefore, future research should continue to develop molecular assays for early and accurate detection of *Clarireedia* pathogens, study their correlation with disease scores, and develop ways to discriminate between all *Clarireedia* species.

Although host resistance can reduce the damage caused by plant pathogens, the cost to renovate turf areas in order to use new resistant cultivars can be substantial, and the durability of the host resistance in these cultivars could be affected by evolutionary changes in pathogen populations. Currently, no information exists on the durability of dollar spot resistance. However, because resistance to dollar spot appears to be polygenic and there appear to be no pathogenic races, this type of resistance is believed to be durable. Resistance breeding for dollar spot management is challenging because of polygenic inheritance and phenotyping constraints. Despite these challenges, turfgrass breeding programs should continue screening diverse turfgrass germplasm to identify sources of dollar spot resistance and incorporate them into breeding programs to develop dollar spot-resistant cultivars.

To date, only a few studies have been conducted on QTL mapping to identify genomic regions associated with dollar spot resistance, and almost all of them were done on creeping bentgrass. Future research should focus on mapping dollar spot resistance genes and QTLs on different turfgrass species (e.g., bermudagrass, seashore paspalum, and zoysiagrass) and identify molecular markers linked to resistance genes or QTLs, which can be used in MAS to quickly incorporate resistance into elite germplasm.

Whole genome sequencing and comparative genomics are powerful approaches to identify pathogenicity factors in fungal pathogens. However, all currently available genome sequences are for *C. jacksonii* and *C. monteithiana* and are fragmented, with variable

length and numbers of scaffolds and contigs (Table 1). Therefore, future research should focus on obtaining complete genome sequences at the chromosome level of all species of *Clarireedia* pathogens. In addition, several genome editing techniques such as clustered regularly interspaced short palindromic repeats/Cas9, transcription activator-like effector nucleases, and zinc finger nucleases have been used to precisely modify the genome of fungal pathogens, allowing manipulation of their phenotypes (Gaj et al. 2016; Muñoz et al. 2019). Genome editing studies of *Clarireedia* spp. with the aim to identify pathogenicity factors, by first targeting known virulence factors, is lacking. Therefore, future research efforts are suggested to focus on these aspects of genomics and genome editing.

Previous research has shown that many fungal pathogens belonging to the Sclerotiniaceae family, a closely related pathogen group to *Clarireedia* spp., produce oxalic acid considered to be a major pathogenicity factor (Andrew et al. 2012; Rioux et al. 2021). On the other hand, many grass species produce oxalate oxidase, which can degrade oxalic acid, limiting successful infection by fungal pathogens. Several studies have demonstrated that transformation of plants with the wheat germin gene (*gf-2.8*) that upregulates oxalate oxidase in plants successfully increases resistance against *S. sclerotiorum* (Donaldson et al. 2001; Dong et al. 2008). However, the function of oxalic acid in the pathogenesis of *Clarireedia* spp. and the role of oxalate oxidase in host resistance are largely unknown. Therefore, future research aiming to better manage this disease should also focus on these aspects of host–pathogen interaction.

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