Integrated Management of Important Soybean Pathogens of the United States in Changing Climate

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Abstract

Soybean (Glycine max L.) is a major crop grown in the United States but is susceptible to many diseases that cause significant yield losses each year. Consistent threats exist across both northern and southern production regions and include the soybean cyst nematode, charcoal rot, and seedling diseases. In contrast, significant soybean diseases like Phytophthora stem and root rot, sudden death syndrome, and Sclerotinia stem rot (white mold) are intermittent threats that can be heavily influenced by environmental factors. Additional threats to soybean production that have emerged in recent years as more common problems in soybean production include root-knot and reniform nematodes, frogeye leaf spot, and Diaportha diseases. Disease in any crop will only occur when the three components of the disease triangle are present: a susceptible host, a virulent pathogen, and a conducive environment. If an environment is becoming more conducive for a particular disease, it is important that farmers and practitioners are prepared to manage the problem. The information in this review was compiled to help assist agriculturalists in being proactive in managing new soybean diseases that may be emerging in new areas. To do this, we provide: 1) an overview of the impact and disease cycle for major soybean diseases currently causing significant yield losses in the United States, 2) a comprehensive review of the current management strategies for each soybean disease, and 3) insights into the epidemiology of each pathogen, including the likelihood of outbreaks and expansion to additional geographic regions based on current trends in climate change.

Key words: soybean, Glycine max, climate change, plant disease, yield loss

Since the year 2000, soybeans (Glycine max L.) have been harvested in the United States from an average 39.6 million hectares (98 million acres) each year, with average yields between 2.7 and 3.4 tonnes per hectare (40 and 50 bushels per acre, assuming one bushel of soybeans weighs 60 lbs.; USDA National Agricultural Statistics Service (NASS) 2020). At an average market value estimated at $330 per tonne ($9 per bushel) during the past 20 yr, annual soybean production is worth over $40 billion (USDA NASS 2020, supplemental file 1). Soybean is valued globally for its relatively high-quality oil and protein, which comprise approximately 20 and 40% of the soybean, respectively (Clemente and Cahoon 2009). The oils are used in cooking and baking, though recent efforts to combat carbon emissions and decrease reliance on fossil fuels have resulted in the utilization of soybean oils as a biodiesel product (Mofijur et al. 2013). Approximately 70% of the soybean value is from meal, 97% of which is used in livestock and poultry feed. Soybean also has many industrial uses, including as important components of adhesives and paints (Raghuvanshi and Bisht 2010).

Given the high volatility in the soybean market and enormous soybean acreage in the United States, farmers are concerned with minimizing soybean yield losses. Unfortunately, soybean is susceptible to many diseases and pests that can cause significant yield...
losses. For example, from 2010 to 2014, soybean yield was reduced by an estimated average of 11.5 million tonnes (421 million bushels) throughout the United States (Allen et al. 2017). In 2018 alone, 14.6 million tonnes (536 million bushels) of soybean were lost due to soybean diseases (CPN 2020, https://loss.cropprotectionnetwork.org/). Major soybean pathogens exist across four domains; fungi, bacteria, nematodes, and oomycetes. The objective of this review article is to highlight the main annual threats, discuss the severe intermittent threats, and point to major emerging threats to soybean production in the United States.

Although potential threats to soybean production vary by growing regions (Allen et al. 2017), some pathogens are consistent causes for concern across both northern and southern production regions. These include the soybean cyst nematode, charcoal rot, and seedling diseases. In contrast, economically significant soybean diseases like Phytophthora stem and root rot, sudden death syndrome (SDS), and Sclerotinia stem rot are intermittent threats that can be heavily influenced by environmental factors. In addition to these diseases, additional disease threats to soybean production have emerged as more common problems in both northern and southern states in recent years. Diseases increasing in frequency include root-knot and reniform nematodes, frogeye leaf spot, and Diaporthe diseases. The economic impact of these diseases has spurred research on their biology, epidemiology, and management. Perhaps the most widespread and consistent threat to soybean production nationwide is the soybean cyst nematode, with 977 peer-reviewed publications over the past two decades (Fig. 1). Similarly, soybean interactions with Phytophthora sojae have revealed an intimate gene-for-gene relationship (Flor 1955), which has driven significant research and publications pertaining to this disease (Dorrance 2018) (Fig. 1). Other significant diseases, like charcoal rot, have received less research attention even though the yield threat remains high (Allen et al. 2017, Fig. 1). In row-crop agriculture, the major disease management strategies include genetic resistance, crop rotation, fungicide and nematicide seed treatments, mid-season fungicide sprays, and biocontrol. Additional cultural practices such as modifications in tillage, row spacing, plant population, and irrigation can also be helpful. Each disease requires a different, and often unique, combination of management strategies for successful disease reduction (Table 1). Because environments can differ from one region to another, some management strategies may be more effective than others in different locations for the same disease.

The environment plays a crucial role in soybean growth and development, and a major study found that an estimated 3.1% soybean yield loss can be expected for each 1°C rise in global mean temperature (Zhao et al. 2017). However, this estimate does not take into account yield losses due to pathogens, which are also affected by the environment. All three aspects of the plant disease triangle must be present for plant disease to occur: a virulent pathogen, a susceptible host, and a conducive environment (Fig. 2).

In each section below, we touch on one of the greatest threats to modern and future agriculture; the shift in global climate patterns and the increased frequency of extreme weather events. Over the next 30 yr, temperatures are predicted to increase 1.5–2°C (2.7–3.6°F) and precipitation is expected to increase in the United States, with many locations already experiencing dramatic changes in weather patterns (Tebaldi et al. 2006, Karl et al. 2009). Predictive modeling for weather systems in the United States estimates that the frequency of convective systems, or very large thunderstorms, will triple by the end of the century, and the total volume of precipitation will increase by 30–80% (Prein et al. 2017). Extreme weather events in 2019 led to heavy rainfall, severe flooding, and approximately 8 million hectares (20 million acres) filed for ‘prevented plant’ insurance coverage, an economic burden of nearly $4 billion (USDA 2019). From 1958 to 2012, the Upper Midwest region of the United States has experienced a 37% increase in precipitation, with trends

Fig. 1. Cumulative publications (articles and reviews) of major soybean diseases since 2000, obtained from Web of Science (webofknowledge.com). Data available upon request.
continuing upwards (Morton et al. 2015). The impacts these types of changes will have on plant diseases are challenging to predict due to the unique disease cycle of each pathogen (Chakraborty and Newton 2011, Garrett et al. 2016, Juroszek et al. 2020), though weather changes are predicted to increase the risk of diseases in the coming decades (Hatfield et al. 2011).

With concerns over changing climate in the 21st century, the environmental component of the disease triangle may also be changing the frequency and severity of disease outbreaks in some regions. In order to prevent a disease, farmers must know if they are at risk for diseases caused by pathogens present in their region, and if their environment is conducive for other pathogens that could enter the area and cause disease. The most significant threats to U.S. soybean production since 2000 have been documented (Allen et al. 2017, Koenn and Wrather 2010), and strategies to manage the major diseases in the United States are covered in this review. Additional soybean diseases that have major effects on soybean production in other countries, such as soybean rust and anthracnose, may also become more significant threats in the United States should climate trends continue as projected (IPCC 2014). Through this review, we aim to provide: 1) an overview of the impact and disease cycle for common soybean diseases in the United States, 2) a comprehensive review of the state of knowledge regarding current management strategies for each soybean disease, and 3) insights into the epidemiology of each pathogen and an indication of the likelihood of outbreaks and spread of major pathogens to new regions based on changing climate trends.

### Consistent Disease Threats to U.S. Soybean Production

#### Soybean Cyst Nematode

**Introduction, Impact, and Disease Cycle**

The soybean cyst nematode, *Heterodera glycines* Ichinohe (Tylenchida: Heteroderidae), is the single greatest threat to soybean yield throughout the United States (Allen et al. 2017). From 2006 to 2014, soybean cyst nematode ranked as the top economic pest of soybean in both northern and southern states, causing an estimated average annual yield loss of over 3.4 million tonnes (125 million bushels) (Allen et al. 2017, Koenn and Wrather 2010). Assuming an average soybean market value of $330 per tonne ($9 per bushel) between 2000 and 2020 (USDA NASS 2020, supplemental file 1), yield loss during that time resulted in an estimated economic loss of over $1.1 billion. The soybean cyst nematode is an obligate, plant-parasitic nematode that resides in many soil types and geographical regions. It can complete its life cycle in 3–4 wk on a susceptible host, resulting in multiple generations and significant increase in nematode population density in a single season (Alston and Schmitt 1988, Anand et al. 1995, Niblack et al. 2006). Foliar symptoms associated with soybean cyst nematode damage are often misdiagnosed as nutrient deficiencies (Niblack et al. 2006), though in many cases aboveground symptoms are lacking altogether, even when soybean cyst nematode is causing significant yield losses (Noel and Edwards 1996, Young 1996, Wang et al. 2003).

The soybean cyst nematode overwinters as eggs encased in a cyst (dead female), which allows them to survive adverse conditions...
in the soil for 10 yr or more (Sipes et al. 1992, Niblack et al. 2006). Under conducive environmental conditions, the eggs hatch and second-stage juveniles (J2) emerge from eggs in search of soybean roots. Ideal hatching conditions include warmer soil temperatures (24–32°C, or 75–90°F) and adequate soil moisture, with the presence of root exudates from soybean or another compatible host enhancing rates of egg hatch (Alston and Schmidt 1988, Anand et al. 1995, Riga et al. 2001). The J2 is the only infective stage of the nematode and moves through the soil in water films that surrounds soil particles until a host root is encountered. It penetrates the root behind the root tip using a specialized mouth part called a stylet, migrates through the cortical tissue toward the plant vascular system, and establishes a feeding site called a syncytium (Niblack et al. 2006). The J2 matures through two other juvenile stages (J3 and J4) at the syncytium before a final molt into adult male or female soybean cyst nematode. Adult females remain sedentary at the feeding site where they enlarge and rupture through the root epidermis, protruding from the roots with the head still located near the feeding cell. Adult males leave the root and return to the soil to mate with one or more female. Females can produce several hundred eggs, most of which remain inside the adult female body, though additional (50 to 100) eggs may be deposited in an external gelatinous matrix called an egg mass (Niblack et al. 2006). When the female dies, her body becomes the cyst, protecting the eggs from environmental factors and prolonging the survival of the eggs.

It is difficult to predict how extreme weather events may affect soybean cyst nematode, as soybean cyst nematode cysts and eggs can survive 10 yr or more without a suitable host (Niblack et al. 2006), and even the juveniles can survive up to 7 mo in flooded soil, up to 29 mo in dry soil, and up to 90 mo in soil at water capacity (Slack et al. 1972). However, as global temperatures are predicted to increase (IPCC 2014), rates of soybean cyst nematode reproduction and egg hatching are likely to increase because low temperatures (15°C or 59°F) inhibit hatching and soybean cyst nematode reproduction (Alston and Schmitt 1988, Anand et al. 1995). Hatching and reproduction of soybean cyst nematode can also be inhibited by extremely high temperatures (≥36°C or 97°F) (Alston and Schmitt 1988), although such high temperatures also inhibit soybean germination by 50% or more (Yagi and Tripathi 1983). Predicted temperature increases could lead to expanding soybean acreage into northern areas where soybeans have not been traditionally grown, though pests and pathogens are also more likely to move poleward with warming global temperatures (Bebbe et al. 2013). Therefore, if temperatures do continue to increase, soybean cyst nematode could become even more problematic in southern states while also becoming more prevalent in northern states, decreasing soybean yields across the United States.

Genetic Resistance

Genetic resistance has been the most popular and effective choice for soybean cyst nematode management. Most of the genetic resistance in commercial soybean lines originate from the plant introduction line PI88788 (McCarville et al. 2017). Although other soybean cyst nematode resistance genes exist in other soybean breeding lines (Concibido et al. 2004, Mitchum et al. 2013), the most common source of resistance is PI88788. Genetic resistance in all resistant lines appears to be quantitative, although the resistance mechanisms and causal genes are not well understood. Resistance in PI88788 is attributed to a quantitative trait locus (QTLs) on chromosome 18, known as Resistance to Heterodera glycines 1 (Rhgl) (Concibido et al. 2004). Interestingly, the Rhgl locus in PI88788 contains many copies of three unrelated genes, and the Rhgl locus in susceptible varieties has fewer copies of these three genes (Cook et al. 2012). Additional QTLs for soybean cyst nematode resistance have been identified, and some of these QTLs overlap with QTLs for resistance to other important soybean diseases (Hughes et al. 2004, Meksem et al. 1999, Strue et al. 2012, Chang et al. 2018, Swaminathan et al. 2018). Identifying additional QTLs associated with strong soybean cyst nematode resistance remains a critical area of research because repeated planting of cultivars with PI88788 resistance resulted in significant selection pressure and the development of soybean cyst nematode populations that can overcome Rhgl resistance (McCarville et al. 2017). In fact, repeated planting of any resistant cultivar can lead to soybean cyst nematode populations adapting to overcome the resistance (Mitchum 2016). Recent efforts to sequence the genome of multiple soybean cyst nematode populations have provided greater insights into mechanisms of soybean cyst nematode virulence (Gardner et al. 2017, Masonbrink et al. 2019a). Collaborative efforts to combat soybean cyst nematode have culminated in an open-access soybean cyst nematode genome browser (scnbase.org, Masonbrink et al. 2019b). These collaborative efforts facilitate more timely discoveries of genetic mechanisms underlying soybean resistance to damaging pests and pathogens.

The ability of soybean cyst nematode to overcome genetic resistance has led to the development of distinct biotypes or races of soybean cyst nematode. A system to characterize these biotypes relative to their ability to reproduce on soybeans containing known sources of resistance, known as the HG typing system, has been developed (Niblack et al. 2002). This HG typing system helps farmers understand what soybean cyst nematode populations they are facing, and which genetically resistant cultivars will be effective in managing soybean cyst nematode in their fields. Selecting cultivars based on this system has been shown to provide a significant yield advantage, particularly with early-maturing soybean cultivars (Wang et al. 2000, Rincker et al. 2017).

Chemical and Biological Control

Chemical control of nematodes and other soilborne pathogens is challenging because proper timing and delivery of the chemistry into the soil are difficult, and chemicals can adversely affect beneficial soil microbes too (Moorman 1989). However, new chemicals developed by agricultural companies have modes of action with increased specificity towards target pathogens that typically require lower rates of active ingredient for successful control. In addition, many chemicals are now formulated as seed treatments, so the chemistry is delivered into the soil along with the seed, which can also reduce rates of active ingredient needed, target the chemistry directly to where it is needed, and protect germinating seedlings. Some common chemicals currently used to manage soybean cyst nematode are abamectin (Avicta, Syngenta Crop Protection, Greensboro, NC), fluopyram (ILEVO, BASF, Ludwigshafen, Germany), pydiflumetofen (Saltro, Syngenta Crop Protection), and tioxazafen (NemaStrike, Bayer CropScience, Kansas City, MO). Abamectin is a natural compound produced by the bacterium Streptomyces avermitilis, and disrupts neuron signaling in nematodes and arthropods (Martin 1997), and is effective against soybean cyst nematode (Viti et al. 2014). Fluopyram is classified as a succinate dehydrogenase inhibitor (SDHI), affecting cellular respiration. Fluopyram has shown efficacy against soybean cyst nematode in addition to several fungal pathogens in field studies, reducing soybean cyst nematode numbers in roots and reducing soybean cyst nematode reproduction in some...
soybean varieties (Kandel et al. 2017, Bissonnette et al. 2020, Roth et al. 2020). Additional lab studies have shown that fluopyram reduces soybean cyst nematode motility and prevents root penetration (Beeman and Tylka 2018, Beeman et al. 2019). Pydflutemotifen and tioxazafen are newer chemistries that have been recently registered for use as nematocide seed treatments in soybean, but reports comparing their efficacy to other products have yet to be made broadly available.

Some microbes compete with soybean cyst nematode for soybean root associations, while others are direct parasites of soybean cyst nematode (Bernard et al. 1996). Specific strains of these microbes have been commercially formulated into seed treatments to aid in the control of soybean cyst nematode and other nematodes. Products such as Votivo (Bacillus firmus strain 1-1582, BASF), Clariva pn (Pasteuria nishizawai strain Pr1, Syngenta Crop Protection), Aveo EZ Nematicide (Bacillus amyloliquefaciens strain PTA-4838, Valen BioSciences, Libertyville, IL), BIOST Nematicide 100 (heat-killed Burkholderia spp. strain A396 cells and spent fermentation media, Albaugh LLC, Ankeny, IA), and Trunemco (Bacillus amyloliquefaciens strain MBI 600 and cis-Jasmone, Nufarm Americas Inc., Alsip, IL) are marketed as nematode control products. The fungus Hirisstella rhossiliensis is parasitic on soybean cyst nematode J2 (Liu and Chen 2001, Chen and Liu 2005, Chen 2007), but has not been commercialized or widely implemented as a biocontrol agent. A recent study by Strom et al. (2020) found that soybean and corn roots host several fungi that release compounds that are toxic to soybean cyst nematode, and that crop rotation and nematode density both can affect fungal communities on soybean roots.

Crop Rotation
Long-term crop rotations that include non-host crops for soybean cyst nematode can reduce soybean nematode population densities and boost soybean yield (Chen et al. 2001a, Niblack 2005, Warnke et al. 2008, Poromarto and Nelson 2010). Non-host crops include wheat, corn, and alfalfa. Soybean cyst nematode can colonize other common legume crops like dry bean (Phaseolus vulgaris), cowpea (Vigna unguiculata), and clover (Trifolium spp.) (Bond et al. 2019). Some common winter annual weeds like chickweed (Stellaria media) bittercress (Cardamine parviflora), purple deadnettle (Lamium purpureum), henbit (L. amplexicaule), penny-cress (Thlapius arvense), shepherd’s-purse (Capsella bursapastoris) can serve as hosts to soybean cyst nematode (Riggs 1992, Venkatesh et al. 2000) and may negate the advantage of crop rotations if the weeds are not well managed (Creech et al. 2008). Unfortunately, since the eggs in soybean cyst nematode cysts can survive for several years in the soil without a host, short-duration rotation sequences such as the popular 2-yr corn–soybean rotation are often insufficient for reducing soybean cyst nematode populations (Koenning et al. 1995).

Cover crops have often been recommended as potential rotational crops, or as ‘trap crops’. Ideally, a trap crop would promote soybean cyst nematode egg hatching and attract J2 to roots, but would not allow soybean cyst nematode to complete its life cycle, thus trapping it inside the root where it would fail to reproduce. Certain crimson clover (Trifolium incarnatum) varieties may attract soybean cyst nematode J2 and some other cover crops may inhibit soybean cyst nematode reproduction in the greenhouse, but the consistency of these effects in the field are often absent (Harbach 2019), and need to be further evaluated with additional field studies.

Tillage
No-till practices can lead to reduced soybean cyst nematode populations at harvest compared to conventional tillage techniques such as diskng, chisel-plowing, and moldboard plowing according to some reports (Tyler et al. 1983, 1987; Workneh et al. 1999; Grabau et al. 2017). However, one study failed to find any impact of tillage or row spacing on soybean cyst nematode population density (Chen et al. 2001b). The presence of wheat residue in the field has been shown to reduce soybean cyst nematode populations at harvest (Hershman and Baci 1995). Tillage with a disc, moldboard plow, or chisel plow has also been shown to affect the ability of different fungal species to parasitize soybean cyst nematode (Bernard et al. 1996), which could potentially contribute to improved soybean cyst nematode control. However, tillage practices alone are insufficient to manage soybean cyst nematode in soybean production systems.

Charcoal Rot
Introduction, Impact, and Disease Cycle
Charcoal rot of soybean is caused by the fungus Macrophomina phaseolina (Tassi) Goid (Botryosphaeriaceae) (Goidanish 1947, Romero Luna et al. 2017). Macrophomina phaseolina is pathogenic on at least 500 plant species, including economically important crops like corn and grain sorghum (Dhingra and Sinclair 1977, 1978; Kunwar et al. 1986). Historically, charcoal rot was a major disease mainly in the southern United States, but the disease has also been reported in northern regions of the United States (Bradley and Rio 2003, Yang and Navi 2005, Wrather and Koenning 2009, Cummings and Bergstrom 2013). In recent years, charcoal rot has consistently been one of the top five yield-reducing diseases of soybean, in both northern and southern U.S. regions (Allen et al. 2017). In 2012, charcoal rot ranked second in yield-limiting soybean diseases across the United States and Canada, causing an estimated yield loss of 2.0 million tonnes (73 million bushels) (Allen et al. 2017).

Macrophomina phaseolina persists in the soil as small, black microsclerotia that germinate between 20°C (68°F) and 40°C (104°F) (Short et al. 1980). The growing mycelia are able to infect roots of seedlings and young plants. Once initial infection has occurred, the fungus grows slowly through the roots and shoots until the soybean plant reaches reproductive stages upon which growth of M. phaseolina rapidly increases. Eventually, vascular tissue becomes clogged by fungal mycelia and microsclerotia, resulting in wilting and premature plant death (Khan 2007). As soybeans are harvested, the newly formed microsclerotia are distributed back into the field with soybean residue, where they will serve as inoculum in following years. Although one study in Brazil demonstrated that microsclerotia could lose their viability after only 5 mo (Reis et al. 2014), it is generally understood that microsclerotia can survive in the soil between 2 and 15 yr (Meyer et al. 1974, Short et al. 1980, Gupta et al. 2012) depending on various environmental and soil factors. Macrophomina phaseolina can also be transmitted through infected seed, which not always obvious as the fungus can be covered by the seed coat (Mengistu et al. 2015).

Genetic Resistance
Efficient means of managing charcoal rot by cultural practices and chemicals are lacking, so a large focus has been placed on the development and characterization of cultivars resistant to M. phaseolina. During the last 20 yr, over 850 soybean genotypes have been screened for resistance to charcoal rot, and 23 were found to have moderate resistance (Mengistu et al. 2007, 2011a, 2013; Pawlowski et al. 2015).
A majority of the resistant genotypes are in maturity group III or later since charcoal rot has historically been a southern disease where later maturity groups are grown. Macrophomina phaseolina has been reported in northern soybean growing regions where it has begun to thrive, possibly due to conducive environments resulting from a warming climate (Bebber et al. 2013). Earlier-maturing soybeans are grown in northern regions, which are more likely to be susceptible to charcoal rot and could help explain the increase in charcoal rot outbreaks in northern states. Recent research has identified resistance in maturity groups between I-III (Scott and Singh 2018). In addition, a recent report identifying potential QTLs in maturity group IV soybeans associated with resistance to M. phaseolina provides the basis for future targeted breeding efforts in soybean (Da Silva et al. 2019).

Crop Rotation
Due to the large number of hosts of M. phaseolina (Livingston 1945), there are few options for rotation with non-host crops for managing charcoal rot. Rotations with cotton can lower the inoculum load in the soil compared to continuous soybean production systems (Francl et al. 1988). Crop rotations with corn can lead to genetically diverse M. phaseolina populations in a field, but these genetically diverse isolates are often still virulent on soybean (Almeida et al. 2008).

Chemical and Biological Control
There is currently not a chemical control method that provides consistent control for charcoal rot (Reznikov et al. 2016). However, biocontrol has shown promise. Seed treated with Rhizobacterium (strain: FPT721) reduced the incidence of disease in one study (Choudhary 2011). In addition, two endophytic bacteria, Paenibacillus (strain: HKA-15) and Bacillus (strain: HKA-121), have shown to be strongly antagonistic to M. phaseolina, suggesting a potential for use as a biocontrol agent against charcoal rot (Senthilkumar et al. 2009). Despite the possibility of control, there are no commercially available biocontrol treatments for charcoal rot at this time.

Cultural Control
The use of irrigation has shown promise for managing charcoal rot (Kendig et al. 2000). High disease severity and yield losses are associated with drought stress, so irrigation may decrease charcoal rot severity in the current year. However, colonization of roots can still occur in asymptomatic soybeans, which may lead to increased quantities of microsclerotia in the soil and greater disease pressure, or increased inoculum, in subsequent years (Kendig et al. 2000, Mengistu et al. 2011b).

The use of tillage has provided inconsistent results across many management studies. Some studies have suggested that tillage can reduce disease by increasing the rate of decomposition of microsclerotia in the soil. Other work has shown that burying microsclerotia deeper than 15 cm (5.9 inches) through tillage decreases microsclerotia germination (Olanya and Campbell 1988, Baird et al. 2003). Some other studies have demonstrated that tillage had no effect on disease pressure or inoculum load compared to no-till systems (Wrather et al. 1998, Mengistu et al. 2009). No-till practices do allow for increased soil moisture retention, though, which could suppress disease since drought stress promotes higher disease development.

Seedling Diseases
Introduction, Impact, and Disease Cycles
Seedling diseases are an annual problem facing soybean farmers across the growing region. This group of diseases is made up of both fungi and oomycetes, with the most common pathogens being Rhizoctonia solani, Fusarium spp., and Pythium spp. (Rizvi and Yang 1996). Often more prevalent in cool and moist years, these diseases result in decreased crop stand either by rotting seeds or by killing the developing seedling soon after emergence, collectively termed ‘damping-off’. Severe damping-off can dramatically decrease crop profitability by forcing farmers to replant entire fields. Between 2010 and 2014, seedling diseases ranked the second or third most yield-limiting disease each year, resulting in estimated losses ranging from 680,000 to 1.7 million tonnes (25 to 64 million bushels) (Allen et al. 2017).

Rhizoctonia solani
Rhizoctonia solani Kuhn (Cantarellales: Ceratosporidiaceae) is the causal organism of Rhizoctonia root rot. Symptoms of this disease are reddish lesions on the hypocotyl of seedlings near the soil line. While this disease can lead to seedling death, some seedlings may survive, resulting in plants with stunted growth. This fungus survives over the winter as sclerotia and mycelia in soil and crop residue, germinating in the spring to infect more plants (Tsror 2010). Rhizoctonia solani is a very genetically diverse fungus, and different genetic backgrounds may be more virulent on different plant hosts (Cubeta and Vilgalys 1997). The R. solani species complex is distinguished by its ability to undergo hyphal fusion with other strains (anastomosis), creating anastomosis groups (AG). The most common AG isolated from soybean roots is AGII-2 (Dorrance et al. 2003). This AGII-2 group thrives better in warmer conditions than other AGs.

Fusarium spp.
Fusarium spp. (Hypocreales: Nectriaceae) are fungi that cause Fusarium root rot. Seedling symptoms of this disease include reddish to brown discoloration of the taproot and lateral roots and reduced nodule formation. If the disease is present in mature plants, aboveground symptoms can include stunting, yellowing, and wilting. Although numerous Fusarium spp. are commonly present in agricultural fields, only a small number are pathogenic to crops (Broders et al. 2007a; Diaz Arias et al. 2011, 2012; Ellis et al. 2013a). These, however, have a wide range of host crops that can be infected. Some of the most common pathogenic species in soybean seedlings are F. solani, F. oxysporum, F. graminearum, and F. acuminatum (Diaz Arias et al. 2013a, Farias and Griffin 1990). Individual isolates of each species may vary greatly in their aggressiveness (Diaz Arias et al. 2013b).

Fusarium spp. favor cool, well-drained soil and are often found infecting plants that have been subjected to severe stress from such factors as herbicide damage, compacted soil, or nematode pressure (Han et al. 2017). Fusarium oxysporum infects through root tips or open wounds and navigates its way to vascular tissue where it will grow upwards in the plant. Other Fusarium species move in the stem outside of vascular tissue. The fungus is capable of surviving for several years in soil and crop residue as chlamydospores or mycelia (Nelson 2015).

Pythium spp.
Pythium spp. (Peronosporales: Pythiaceae) Pringsheim belongs to a lineage of fungus-like microorganisms called oomycetes. In soybean, Pythium spp. can cause seed rot, seedling blight, root rot, and damping-off. This disease occurs most often in cool (<18°C or 64°F) and wet soils (Rothrock et al. 2015). Symptoms of infected seedlings include development of water-soaked lesions, which initially appear on the hypocotyl or cotyledons, and rotten roots that
make the seedlings easy to pull from the soil. *Pythium* spp. survive in the absence of a host as oospores in the soil or in crop residue. When the soil is saturated with water, these oospores produce fruiting bodies (sporangia), which release motile zoospores that move through water films and infect plants. Once infection and colonization of soybean root tissue have occurred, more oospores are produced, and the cycle continues. A wide variety of *Pythium* spp. vary in their aggressiveness across different crops. For instance, some are more aggressive on soybeans than corn, whereas others are more aggressive on corn than on soybean. (Broders et al. 2007b; Rojas et al. 2017a,b). Temperature affects the virulence of different *Pythium* spp. (Matthiesen et al. 2016, Rojas et al. 2017a), and as global temperatures potentially increase, there may be a shift in the virulent *Pythium* spp. commonly causing damping-off in soybean.

**Genetic Resistance**

To date, there are no soybean varieties with strong genetic resistance to *Fusarium* spp. However, resistance to *Pythium* has been identified and characterized in the soybean line Archer with the initial resistance gene named *Rpa1* (resistance to *P. aphanofermatum-1*) (Bates et al. 2008, Rosso et al. 2008). Since the discovery of *Rpa1*, additional QTLs have been identified for both qualitative and quantitative resistance (Rosso et al. 2008, Ellis et al. 2013b, Urrea et al. 2017, Lin et al. 2018). In addition to resistance in soybean, the incidence of disease caused by *Pythium* spp. was reduced in certain soybean cyst nematode-resistant cultivars, which may indicate some cross-resistance mechanisms present in soybean (Murillo-Williams and Pedersen 2008). The transgenic introduction of antifungal genes into potato decreased the level of disease caused by *R. solani*, suggesting the possibility of transgenic approaches in soybean to prevent losses from Rhizoctonia root rot (Fernandez Bidondo et al. 2019).

**Crop Rotation**

Crop rotation has shown only limited utility for seedling disease management. These pathogens have a large number of alternative hosts, and some have been isolated from both agronomic crops and weed species (Jager et al. 1982, Carling et al. 1986, El Bakali et al. 2000). Since all three genera of seedling pathogens are capable of infecting both soybeans and corn, a corn–soybean crop rotation is unlikely to eliminate these pathogenic species from a field (Summer and Bell 1982; Leslie et al. 1990; Zhang and Yang 2000; Dorrance et al. 2004a; Broders et al. 2007a, b, Murillo-Williams and Pedersen 2008). An interesting, but largely unexplored concept is that crop rotation may alter the soil microbiome or increase the population of microorganisms that are antagonistic to plant pathogens, which could lead to future management strategies (Rojas et al. 2019).

**Chemical and Biological Control**

The use of fungicide seed treatments is most effective when planting occurs early in the season when soil temperatures are low, under wet conditions, in reduced tillage fields, or in fields with a history of seedling diseases. Commonly used fungicide or oomicide seed treatments and their general effectiveness on soybean seedling and root pathogens have been summarized and made publicly available (CPN 2019). Some seed treatments prevented stand loss caused by *R. solani* but did not completely prevent yield losses (Dorrance et al. 2003). In the laboratory, most *R. solani* isolates collected from soybeans were sensitive to SDHI fungicides, but they may or may not be sensitive to demethylsation inhibitor (DMI) fungicides (Ajayi-Oyetunde et al. 2017). In the greenhouse, both SDHI and DMI fungicide seed treatments appear to be effective at controlling Rhizoctonia root rot (Ajayi-Oyetunde et al. 2017). For *Fusarium* spp., the active ingredient fluoxystrobin was more effective in decreasing mycelial growth than other common fungicide seed treatments, including azoxystrobin, trifloxystrobin, and captan (Broders et al. 2007a). However, there have been multiple reports of resistance to fluoxystrobin in *Fusarium* spp. isolates. Due to the recent increase in available oomicide products across different chemical classes, seed treatments with oomicides for controlling *Pythium* in soybean has become more common (Broders et al. 2007a, b; Bradley 2008; Peters et al. 2008; Matthiesen et al. 2016; Scott et al. 2020). Unfortunately, across fungicide and oomicide classes, some pathogen populations have inherent resistance to certain fungicides, and other populations can develop or acquire resistance to these fungicides (Noel et al. 2019, Peng et al. 2019). The Fungicide Resistance Action Committee (FRAC) monitors pathogen resistance to fungicides over time according to the different modes of action of each chemical class and provides guidance for their most effective use (Brent and Holllomon 2007).

The use of organisms such as binucleate Rhizoctonia spp. and Actinomycete bacteria as biological control agents have shown promise in suppressing the growth of *R. solani* (Escande and Echandi 1991, Tuitert et al. 1998). Another antagonist, *Verticillium biguttatum*, parasitizes *R. solani* and suppresses sclerotial development, resulting in decreased inoculum in the following years (Van den Boogert et al. 1989, Jager et al. 1991, Van den Boogert and Deacon 1994). *Trichoderma harzianum* colonization leads to reduced disease symptoms caused by both *R. solani* and *F. oxysporum* (Siven and Chet 1986, 1989; Tsror et al. 2001; Thangavelu et al. 2004), while *T. veride* reduced disease severity caused by *F. oxysporum* f. sp. adzuki and by *Pythium arachnoideum* (John et al. 2010). The use of *Pseudomonas putida* strain NIR as a seed treatment on soybeans lowered the incidence of damping-off caused by *Pythium ultimum* at temperatures above 12°C (53°F) (Paulitz 1991, Paulitz et al. 1992). Unfortunately, while this has been an active area of research, commercial formulations of these biological agents have not been widely marketed.

**Cultural Control**

High soil moisture is critical for the development of seedling diseases caused by *Pythium* spp. and *R. solani*, and the current climate trends in much of the soybean production area includes increased soil moisture and temperatures, especially during the spring planting season (Delgado-Baquerizo et al. 2020). The installation of large-scale tile drainage systems has the potential for reducing the retention of soil moisture, which could help alleviate the risk of infection by *Pythium* spp. and *R. solani*. However, this approach might also increase the risk of seedling disease caused by *Fusarium* spp., which prefer well-drained soils (Han et al. 2017).

Reduced or no-till practices have been growing in popularity for soybean production due to many positive benefits for soil conservation (Uri 2000). A result of reduced tillage is increased retention of soil moisture. This moisture would then be available for soybean germination and early growth, but it might also promote a microenvironment more conducive for seedling diseases. Additionally, minimum or no-till soil conservation practices also allow for the retention of crop residue on the soil surface, potentially favoring the survival of these species (Leslie et al. 1990).
Intermittent Disease Threats to U.S. Soybean Production Heavily Influenced by Environmental Factors

Phytophthora Root and Stem Rot

Introduction, Impact, and Disease Cycle

For many years, *Phytophthora sojae* Kaufm. & Gerd. (Peronosporales: Peronosporaceae) has been recognized as a major threat to soybean production (Kaufmann and Gerdemann 1958). This pathogen caused an estimated average soybean loss of over one million tonnes (37 million bushels) per year from 2006 to 2014 (Allen et al. 2017, Koening and Wrather 2010). *Phytophthora* spp., like *Pythium* spp., are oomycetes, sometimes referred to as ‘water-molds’ (Tyler 2007). *Phytophthora sojae* overwinters as oospores that are relatively large and durable compared to its other life stages (Dorrance 2018). During times of high moisture like heavy precipitation, irrigation, or flooding events, the oospores germinate to form sporangia, which are packed with zoospores. These zoospores are smaller than oospores and are also mobile, containing two flagella for swimming (Morris and Ward 1992, Dorrance 2018). When a zoospore comes in contact with a soybean root, the flagella detach and the zoospore directly infects the root (Tyler 2007). While *P. sojae* is soilborne and primarily infects roots, it is capable of infecting any part of a soybean plant at any age (Tyler 2007).

Infection of soybean by *P. sojae* results in root and stem rot. Severe colonization of the root and stem of a young seedling often results in damping-off, or premature wilting and death (Tyler 2007, Dorrance 2018). On mature plants, *P. sojae* infection results in water-soaked lesions on the stem and significant root rotting in susceptible cultivars (Schmitthenner 2000). Other species in the *Phytophthora* genus are also significant pathogens of certain crops and trees, with differences in host range typically attributed to differences in the plant’s ability to recognize the pathogen (Cui et al. 2015, Wang and Jiao 2019). Rojas et al. (2017a) identified other species of *Phytophthora*, including *P. sansomeana* and *P. drechsleri*, that are capable of colonizing soybean seedlings and causing root rot, but it is unknown to what extent these species cause root rot and damping-off compared to *P. sojae*. It is known that temperature has a significant effect on the pathogenicity of oomycete pathogens in general (Matthiesen et al. 2016), with *P. sojae* being significantly more aggressive at 20°C than 13°C (Rojas et al. 2017a). If temperatures continue to increase and coincide with severe flooding in soybean production areas, disease pressure and *P. sojae* abundance are likely to increase.

Genetic Resistance

The host range for *P. sojae* is quite limited, and soybean is the only economically important host (Schmitthenner 2000, Tyler 2007). Specific resistance genes in soybean, called resistance to *Phytophthora sojae* (Rps) genes, are responsible for resistance to various races of *P. sojae* based on specific genes present and expressed by *P. sojae* (Birch et al. 2006). To date, 33 Rps genes have been identified in various soybean cultivars (Table 2) (Sahoo et al. 2017, Zhong et al. 2019). Six of these genes are commonly found in commercial cultivars and provide good disease management against *Phytophthora* root and stem rot (Table 2) (Robertson et al. 2009, Slaminko et al. 2010, Dorrance 2018). These Rps genes contribute to a very robust qualitative resistance against specific races of *P. sojae* (Dorrance et al. 2004b). Additionally, soybeans may also contain genes that contribute to partial resistance, even though they are not classical *Rps* genes. These genes provide partial resistance through mechanisms such as the development of fewer lesions, smaller lesions, or allowing reduced oospore production (Mideros et al. 2007, Dorrance 2018).

Crop Rotation

Soybean is commonly rotated with corn and wheat, which are non-hosts for *P. sojae*. Rotating soybean with corn or wheat resulted in a more diverse population of *P. sojae*, comprised of less virulent races than when soybean was grown in monoculture (Li-ming et al. 2016). However, due to the high persistence and survivability of oospores in the soil, long-term crop rotations are more likely to limit *P. sojae* disease than 2-yr corn–soybean or wheat-soybean rotations.

Chemical and Biological Control

Many chemistries have shown efficacy in managing *P. sojae* (CPN 2019). One common fungicide with activity against oomycetes (oomicide) that is used in commercial seed treatments is metalaxyl, or its purified active isomer, mefenoxam (Monkiedje and Spiteller 2002, Dorrance 2018). The exact mechanism by which mefenoxam is toxic to oomycetes is unknown, though evidence suggests that it inhibits RNA polymerase and prevents oomycetes from expressing genes necessary for survival (Davidse et al. 1983, Parra and Ristaino 2001). Seed treatments containing metalaxyl or mefenoxam have shown efficacy against *P. sojae*, particularly in areas that have received heavy rainfall or irrigation shortly after planting (Dorrance et al. 2009).

Other chemistries, including ethaboxam and oxathiapiprolin, are registered as seed treatments and have demonstrated efficacy against certain oomycete species in the laboratory (Ji and Cisinos 2015, Radmer et al. 2017). Some oomycete species were discovered to have inherent resistance to ethaboxam (Noel et al. 2019), and this resistance was genetically engineered in the laboratory, conferring ethaboxam resistance in *P. sojae* (Peng et al. 2019). Similar genetic experiments in oomycetes have conferred resistance to oxathiapiprolin (Pasteris et al. 2016, Miao et al. 2018). To date, no *Phytophthora* isolates have been identified as having inherent resistance to either ethaboxam or oxathiapiprolin in the field, so the use of these chemistries as seed treatments holds promise for controlling Phytophthora root and stem rot. However, repeated use of these chemistries could select for natural mutations that confer resistance to these chemistries in the field, so good stewardship is necessary to maintain the efficacy of these newer chemistries.

Biocontrol of *Phytophthora* is an active area of research (Xiao et al. 2002, Arfaoui et al. 2018, Wagner et al. 2018, Liu et al. 2019), but no commercial formulations or seed treatments are currently being marketed for widespread use in soybean fields. Many scientists are investigating microbiomes and attempting to isolate new microbes that show beneficial activity towards reducing crop diseases, including Phytophthora stem and root rot (Boscaiu et al. 2019).

Cultural Control

*Phytophthora sojae* requires free water to complete its life cycle effectively (Tyler 2007). The water allows motile zoospores to swim towards soybean roots efficiently. Therefore, heavy irrigation is not recommended in fields with a history of Phytophthora stem and root rot. Increased soil drainage using tillage or field tile can significantly reduce disease caused by *P. sojae* (Kittle and Gray 1979, Dirks et al. 1980, Schmitthenner 1985, Dorrance et al. 2009).
Sudden Death Syndrome

Introduction, Impact, and Disease Cycle

Soybean SDS was first observed in the United States in 1971 in Arkansas, but the causal agent was not identified until the late 1980s (Roy 1997, Roy et al. 1989, Rupe 1989). In the United States, SDS caused an estimated average soybean yield loss of 750 thousand tonnes (27.7 million bushels) between 2004 and 2009, and an estimated average yield loss of 1.1 million tonnes (41.9 million bushels) between 2010 and 2014 (Wrather and Koenning 2009, Koenning and Wrather 2010, Allen et al. 2017). Originally described as Fusarium solani f. sp. glycines, subsequent studies of this pathogen revealed that F. solani f. sp. glycines was actually multiple different species. To date, seven SDS-causing species have been identified; Fusarium virguliforme (Aoki et al. 2003), F. tucumanae (Aoki et al. 2003), F. brasiliense (Aoki et al. 2005), F. cuneirostrum (Aoki et al. 2005), F. eugnum (Aoki et al. 2012a), F. crassistipitatum (Aoki et al. 2012b), and an unnamed species in South Africa (Tewoldemedhin et al. 2017). In the United States, F. virguliforme O’Donnell & T. Aoki (Hypocreales: Nectriaceae) is the most prominent SDS-causing species, although recent surveys have also identified F. brasiliense and F. cuneirostrum in Michigan infecting soybean and dry bean (Jacobs et al. 2018, Wang et al. 2019).

SDS-causing pathogens reduce yield in two-phases of disease. In the first phase, symptoms appear in the roots at the site of infection as discoloration and rotting. As infection progresses deeper into the root, the pathogen releases toxins and proteins that cause foliar symptoms, the second phase of the disease. Foliar symptoms appear as interveinal chlorosis that develops into necrosis,

### Table 2. Genes and sources for resistance to Phytophthora sojae

| Allele | Source(s) | Deployed in commercial lines | Citation |
|--------|-----------|-----------------------------|----------|
| Rps1a  | Mukden    | Yes                         | Bernard et al. 1957 |
| Rps1b  | PI84637   | No                          |          |
|        | D60-9647  | No                          |          |
|        | Sanga     | No                          |          |
|        | Harrell   | Yes                         |          |
| Rps1c  | PI54615-1 | Yes                         |          |
|        | PI86050   | No                          |          |
|        | PI229342  | No                          |          |
|        | Lee68     | Yes                         | Mueller et al. 1978 |
| Rps1d  | PI103091  | No                          | Hartwig et al. 1968 |
| Rps1k  | Kingwa    | No                          |           |
| Rps2   | CNS       | No                          |           |
| Rps3a  | PI68972-1 | Yes                         |           |
|        | P1171442  | No                          |           |
| Rps3b  | P1172901  | No                          |           |
|        | P182.312N | No                          |           |
| Rps3c  | PE340046  | No                          |           |
| Rps4   | PI86050   | No                          |           |
| Rps5   | L62-904   | No                          |           |
|        | P11160    | Yes                         |           |
| Rps6   | Altona    | Yes                         |           |
| Rps7   | Harosoy   | No                          |           |
| Rps8   | PI399073  | No                          |           |
| Rps9   | Ludou 4   | No                          |           |
| Rps10  | Wadou 15  | No                          |           |
| Rps11  | PE594257  | No                          |           |
| RpsUN1 | PE57139B  | No                          |           |
| RpsUN2 | PE57139B  | No                          |           |
| RpsYu25| Yudou 25  | No                          |           |
| RpsYD29| Yudou 29  | No                          |           |
| RpsYD25| Yudou 25  | No                          |           |
| RpsYB30| Yobian 30 | No                          |           |
| RpsZS18| Zaoshu18  | No                          |           |
| RpsSN10| Suinong 10| No                          |           |
| Rps1  (new allele) | Wasehito  | No                          |           |
| RpsJS | Nannong 10-1 | No                       |           |
| RpsWY | Wayao     | No                          |           |
| RpsHC18| Huachun 18| No                          |           |
| RpsX  | Xiu94-11  | No                          |           |
| RpsQ  | Qichadou 1| No                          |           |
| RpsHN | Meng8206  | No                          |           |
| RpsGZ | Guiza01   | No                          |           |

Adapted from Grau et al. (2004) and Dorrance et al. (2004b) updated with current literature.
ultimately leading to premature leaf drop and pod abortion (Hartman et al. 2015). The foliar symptoms typically occur at or after flowering and are exacerbated by high soil moisture resulting from heavy rain events or excessive irrigation during flowering (Leandro et al. 2013). Foliar symptoms can develop prior to flowering in areas with high inoculum density of F. virguliforme (Roth et al. 2019). While the foliar symptoms are characteristic of the disease and visually striking, the pathogen remains in the roots where it forms asexual conidia for dissemination and chlamydospores that serve as overwintering inoculum (Roy 1997, Aoki et al. 2003). Soybean SDS and the soybean cyst nematode are commonly found in the same fields, each capable of reducing soybean yield independently (Hershman et al. 1990, Rupe et al. 1993, Marburger et al. 2014). However, the presence of soybean cyst nematode enhances SDS symptoms caused by F. virguliforme (McLean and Lawrence 1995, Xing and Westphal 2013, Westphal et al. 2014, Brzostowski et al. 2018, Roth et al. 2019) and successful soybean cyst nematode management can reduce SDS severity (Kandel et al. 2017). Climate models include an increased frequency of heavy rain events in association with higher temperatures (Mallakpour and Villarini 2015), and together these conditions may increase the incidence and severity of soybean SDS. If soil temperatures increase to 29°C or higher, SDS severity could decrease (Gongora-Canul and Leandro 2011).

Genetic Resistance

Genetic resistance to SDS is complex and controlled by QTLs (Swaminathan et al. 2016, Chang et al. 2018). Each QTLs can contribute to specific aspects of SDS development, including root infection and foliar symptoms (Kazi et al. 2008, Luskew et al. 2013, Tan et al. 2019). Some SDS QTLs overlap with QTLs associated with resistance to other soybean diseases (Meksem et al. 1999, Hughes et al. 2004, Srour et al. 2012, Swaminathan et al. 2018). Investigations into additive and epistatic genetic relationships have led to improvements in molecular-assisted breeding efforts and a proposed mechanism of SDS resistance in soybean roots (Zhang et al. 2015). Breeding efforts for developing partially resistant varieties have been partially successful, as certain varieties are more resistant to SDS than others in the field (Kandel et al. 2016 2017). Transgenic approaches to incorporate SDS resistance into soybean include transgenic expression of killer proteins (Lightfoot 2015) to limit F. virguliforme infection, transgenic expression of receptor-like kinases (Srour et al. 2012), and transgenic expression of antibodies that recognize and sequester F. virguliforme toxins (Brar and Bhattacharyya 2012). Another avenue of resistance may be obtained through editing of STAY-GREEN genes that have been shown to confer susceptibility to F. virguliforme toxins (Chang et al. 2019). Transgenic approaches hold promise for improving SDS in the future, but these traits are not currently available in soybean cultivars.

Crop Rotation

Long-term crop rotations of 3–4 yr away from soybean can reduce F. virguliforme abundance five-fold compared to the 2-yr corn–soybean rotation commonly used by farmers (Leandro et al. 2018). However, this reduction in F. virguliforme inoculum is dependent on the crops used in the rotation and weed pressure. Fusarium virguliforme can colonize at least 15 crop and weed species, and can survive long-term in corn residue (Kolander et al. 2012, Navi and Yang 2016). Unfortunately, most farmers do not commonly adopt long-term crop rotations with diverse crops due to various economic and practical reasons.

Chemical and Biological Control

Fungicide seed treatments have become popular in recent years in soybean cropping systems. Fungicides classified as SDHI, like fluopyram (ILEVO, BASF), have shown efficacy against SDS-pathogens in lab experiments (Wang et al. 2017, Sang et al. 2018). When used as a seed treatment, fluopyram reduces SDS foliar severity (Kandel et al. 2016, 2017, 2018; Sjarpe et al. 2020) and root rot severity (Sjarpe et al. 2020) while also protecting yield potential in field trials. However, other fungicide seed treatments have not shown the same benefit (Weems et al. 2015, Kandel et al. 2019a). Since the pathogen persists in the soil and below-ground plant parts, mid-season foliar fungicide sprays are not efficacious (Kandel et al. 2019a). Another recently registered product, pydiflumetofen (Salto, Syngenta Crop Protection), has shown some efficacy, but field data are limited.

Root colonization, root rot, and foliar SDS symptoms caused by F. virguliforme are reduced when soybean roots are pre-colonized by the mycorrhizal fungi Rhizopogon irregularis and R. intraradices (Marquez et al. 2019, Pawlowski and Hartman 2020). A similar study found that some Trichoderma harzanium isolates can inhibit F. virguliforme growth and root rot (Pimentel et al. 2020). The mechanisms of these potential biocontrol agents may be related to priming of defense response genes, secondary metabolism, or stress signaling. However, these potential biocontrol applications have not been developed into commercially available products to date.

Cultural Control

SDS commonly occurs first in areas with high levels of compaction, such as low-lying areas or headlands (Roy et al. 1997, Vick et al. 2003), so breaking up soil compaction may reduce SDS incidence and severity. Conventional tillage has shown reductions in SDS compared to no-till (Wrather et al. 1995; Vick et al. 2003, 2006), though one report found that tillage had no effect on SDS (Kandel et al. 2019b).

Early regional risk prediction models have been developed for soybean SDS using environmental data and geographic location to predict the likelihood of SDS reaching various regions of the United States (Scherm and Yang 1996, 1999; Scherm et al. 1998). Although regional models suggested that SDS would not likely be prevalent in northern U.S. states, the disease has been found as far north as North Dakota (Nelson et al. 2019). More recent efforts to model SDS development at an individual field level have incorporated pathogen abundance data (Roth et al. 2019), but forecasting models for SDS are not yet available.

Sclerotinia Stem Rot

Introduction, Impact, and Disease Cycle

Sclerotinia sclerotiorum (Lib.) de Bary (Helotiales: Sclerotiniaceae) is capable of infecting over 400 species of plants. In soybean, the pathogen causes the destructive disease Sclerotinia stem rot, also known as white mold (Boland and Hall 1994). Sclerotinia stem rot can lead to economic losses for farmers by reducing the number of seeds, seed weight, and seed quality (Hoffman et al. 1998, Danielson et al. 2004). While being ranked in the top 10 most yield-limiting diseases of soybean from 2010 to 2013, a severe Sclerotinia stem rot outbreak in 2014 led to a top-five ranking in that year (Allen et al. 2017). The increase in severity was largely due to weather conditions that were conducive for severe Sclerotinia stem rot (Fall et al. 2018a). Sclerotinia sclerotiorum is favored by cool and moist conditions and is prevalent in the Upper Midwest where such conditions are common. Increasing average temperatures and more frequent

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rainfall events leads to higher humidity, and in the northern soybean production belt, these conditions may increase the frequency of Sclerotinia stem rot (Bebber et al. 2013). Incidence and severity in some traditionally problematic regions may also decline due to increasing temperature trends that limit pathogen development.

Sclerotinia stem rot first appears on soybean as white, fuzzy mycelia on the main stem and lateral branches beginning around the R5 growth stage. This white growth is where the term ‘white mold’ is derived. However, the pathogen first begins its life cycle in the soil as melanized, seed-like survival structures called sclerotia. These sclerotia require a 1- to 2-wk-period of soil moisture at a water potential of around −100 kPa, and an extended cool period of 8–21°C (46–70°F) in order to germinate (Clarkson et al. 2004, Michael et al. 2020, Shahoveisi and del Río Mendoza 2020). Apothecia, which are the fruiting structures, resemble tiny, tan mushrooms, with a cup-like cap where ascospores develop (Phillips 1986, Dillard et al. 1995). In addition to the environmental conditions mentioned above, apothecial development from sclerotia also requires canopy closure and proper light quality, between 276 and 319 nm (Thaning and Nilsson 2000; Fall et al. 2018b). Once these conditions are met, apothecia begin forming from sclerotia present within the top 2–3 cm (0.8–1.2 inches) of the soil. When fully mature, apothecia are exposed to a slight decrease in moisture tension, commonly occurring after the morning dew dries, ascospores are forcibly ejected into the crop canopy (Abawi and Grogan 1979). Under controlled laboratory conditions, apothecia exposed to humid environments continuously release ascospores, peaking after 36 h, but ascospore release in the field occurs in the morning dew dries, ascospores are forcibly ejected into the crop canopy (Phillips 1986, Dillard et al. 1995). In addition to the environmental conditions mentioned above, apothecial development from sclerotia also requires canopy closure and proper light quality, between 276 and 319 nm (Thaning and Nilsson 2000; Fall et al. 2018b). Once these conditions are met, apothecia begin forming from sclerotia present within the top 2–3 cm (0.8–1.2 inches) of the soil. When fully mature, apothecia are exposed to a slight decrease in moisture tension, commonly occurring after the morning dew dries, ascospores are forcibly ejected into the crop canopy (Abawi and Grogan 1979). Under controlled laboratory conditions, apothecia exposed to humid environments continuously release ascospores, peaking after 36 h, but ascospore release in the field follows a diurnal pattern with the highest levels of release occurring around midday (McCartney and Lacey 1991, Clarkson et al. 2003). Ascospores, the primary source of inoculum, land on senescing plant parts and germinate when the temperature is between 15 and 25°C (59–77°F) and leaves have been wet for 2–4 h (Young et al. 2004). The fungus most often infects through senescing flowers, and rarely through wounds, natural openings, and contact with neighboring plants (Grau and Hartman 2015).

Genetic Resistance
Genetic resistance to Sclerotinia stem rot, which has been identified in both germplasm screening and QTLs mapping, is a tool for control of the disease (Huynh et al. 2010; Bastien et al. 2014; Zhao et al. 2015; McCaghey et al. 2017, 2019). However, the development of resistant cultivars has been challenging due to the quantitative nature of the resistance (Arahana et al. 2001, Vuong et al. 2008). Although genetic mechanisms of resistance to S. sclerotiorum remain unknown, it appears that specific regulation of genes in the phenylpropanoid pathway may enhance resistance to S. sclerotiorum (Ranjan et al. 2019). Research efforts have also been made to discover genes related to soybean traits that would allow them to evade infection, such as reduced lodging, increased plant height, and altering plant maturity (Kim and Diers 2000).

A difficulty in breeding for resistance to Sclerotinia stem rot is the heterogeneity of S. sclerotiorum distribution in fields during screening and evaluation, that could lead to type I errors (false positives) when performing disease ratings. In addition, there may also be S. sclerotiorum population differences between geographic locations where field screenings occur (Attanayake et al. 2013, Aldrich-Wolfe et al. 2015). For example, in 2017 one particular cultivar had a disease incidence of 10% at a location in southern Wisconsin and 68% at a location in northern Wisconsin (S. Conley, personal communication), possibly due to differences in genetically diverse S. sclerotiorum populations (Attanayake et al. 2019). In order to account for these genotype and environment interactions, it has been suggested that new soybean breeding lines should be screened using a panel of nine isolates of varying aggressiveness to identify overall resistance levels (Willbur et al. 2017).

Crop Rotation
Crop rotation is unlikely to be highly effective for Sclerotinia stem rot Management (Mueller et al. 2002b). Sclerotia can remain viable in the soil for up to 8 yr, and S. sclerotiorum has a wide host range (Adams and Ayers 1979). Crop rotation is unlikely to lower sclerotial density in a field sufficiently to manage disease incidence, although one study showed that corn and wheat could reduce the number of apothecia present in a field (Gracia-Garza et al. 2002).

Chemical and Biological Control
The registered fungicide classes for Sclerotinia stem rot management include methyl benzimidazole carbamates (MBC), DMI, SDHI, quinone outside inhibitor (QoI), and 2,6-dinitro-anilines (Willbur et al. 2019a,b). Fungicides should be sprayed at the R1-R3 growth stages to prevent S. sclerotiorum from infecting senescent flowers (Mueller et al. 2002a). Fungicide programs with either boscalid or picoxystrobin resulted in the greatest disease suppression and the highest yield (Willbur et al. 2019b). Yield losses occur when a disease severity index of 20–25% has been reached, with substantial losses occurring around 68% (Willbur et al. 2019b). Interestingly, the application of the herbicide lactofen for post-emergence broadleaf weed control has decreased Sclerotinia stem rot incidence in high disease locations (Dann et al. 1999). Application of lactofen decreases Sclerotinia stem rot incidence by delaying the closure of plant canopy and stimulating soybean production of glyceollin, a phytoalexin, that has known antifungal activity (Kim et al. 2010).

Coniothyrium minitans, a fungal pathogen of S. sclerotiorum, infects sclerotia in the soil leading to reduced inoculum load or pathogen abundance (Huang and Hoes 1976). Coniothyrium minitans, commercially formulated as Contans WG (Bayer CropScience), reduced disease severity by 68% and degraded up to 95% of sclerotia (Smolinska and Kowalska 2018). A second potential biological control agent, Sporidesmium sclerotiorum, led to a decrease of Sclerotinia stem rot in field trials in Iowa (del Rio et al. 2002). Two other biological agents that show promise for reducing Sclerotinia stem rot incidence are Streptomyces lydicus and Trichoderma harzianum, both of which were able to reduce disease severity by 43 and 38% and degraded sclerotia in the soil up to 90 and 70%, respectively (Zeng et al. 2012).

Cultural Control
High plant populations of >432,000 plants per hectare (175,000 plants per acre) have been shown to result in a greater severity of Sclerotinia stem rot, because dense plant stands decrease airflow and increase moisture retention in the plant canopy creating a conducive environment for apothecia germination and disease (Lee et al. 2005, Fall et al. 2018b). Wide row spacings of 76 cm (30 in) lowered disease severity index compared to row spacings between 25 and 38 cm (10–15 in) (Grau and Radke 1984). Narrow row spacings likely result in higher disease severity due to quicker canopy closure, which promotes apothecial formation and increases the risk of Sclerotinia stem rot development (Fall et al. 2018b). The use of irrigation has been shown to increase Sclerotinia stem rot in soybean, likely by providing the moisture that sclerotia need to germinate. Limiting irrigation during growth stages when flowers are present results in less disease compared to biweekly irrigation throughout the entire season (Grau and Radke 1984).
Results have been inconsistent for different tillage practices on reducing Sclerotinia stem rot (Gracia-Garza et al. 2002, Mueller et al. 2002b). Moldboard plowing has been shown to reduce the density of sclerotia in the upper horizons of the soil, leading to decreased or delayed apothecial germination. However, plowing in subsequent years can bring viable sclerotia back to the surface (Mueller et al. 2002b). As agriculture has shifted toward more sustainable practices, cover crops have become an area of research focus. Cover crops might prevent the production of apothecia and the release of ascospores into the soybean canopy. A recent study indicated that planting soybeans into rolled-crimped cereal rye reduced the incidence of Sclerotinia stem rot due to the production of nonfunctional apothecia (Pethybridge et al. 2019). With the wide host range of S. sclerotiorum; however, it is unclear how many more cover crops may have a similar effect and how many may even lead to an increase in disease levels.

Predictive Modeling

The use of fungicides is expensive, so using them only when disease risk is high is the most cost-effective. Epidemiological modeling of Sclerotinia stem rot development can help farmers determine the ideal timing for fungicide application (Willbur et al. 2019b). Multiple predictive models for Sclerotinia spp. have been developed for various cropping systems, including canola, lettuce, and peanut (Bom and Boland 2000, Smith et al. 2007, Clarkson et al. 2014). For Sclerotinia stem rot management in soybean, the prediction of apothecia presence has been used to predict the likelihood of disease based on work showing that the location of apothecia in a field is strongly correlated with local disease incidence (Wegulo et al. 2000). Two Sclerotinia stem rot models have been created, one in irrigated soybeans and one in a non-irrigated crop. Using weather conditions as predictor variables, these two models show an acceptable precision in the prediction of apothecial presence with an accuracy between 67 and 70% during soybean flowering stages (Willbur et al. 2018a). The most recent Sclerotinia stem rot model was validated across multiple locations in multiple states and continues to be refined (Willbur et al. 2018b). These models are vital in assisting farmers in the fungicide decision-making process.

Increasing Disease Threats to U.S. Soybean Production From Pathogens Moving to New Regions

Plant-Parasitic Nematodes

Introduction, Impact, and Disease Cycles

Plant-parasitic nematodes cause an estimated $78 billion worth of damage on soybean worldwide each year (Lima et al. 2017). Nematodes other than soybean cyst nematode are a common threat to soybean production in southern states and are becoming of increasing concern in northern soybean growing regions. Allen et al. (2017) reported that nematodes other than soybean cyst nematode ranked in the top three most yield-limiting pathogens annually from 2010 to 2014, accounting for an estimated yield loss of over 1.5 million tonnes (55 million bushels). Combined with soybean cyst nematode, plant-parasitic nematodes reduced soybean yield potential by an average of 31% (Allen et al. 2017). All nematodes that affect soybean are soilborne and feed on the root system, limiting water and nutrient uptake from the soil. Although their life cycles are somewhat similar, each nematode species differs in feeding behavior, damage to soybean, and distribution across the United States.

In general, extended periods of warm temperatures increase nematode reproduction. Projected increases in temperatures associated with climate change during the cropping season are likely to favor nematode reproduction and their subsequent impact on soybean production.

The basic life cycle of plant-parasitic nematodes consists of an egg stage, four juvenile stages, and the adult male and female. Eggs may be deposited as a single egg or in masses in the soil, inside roots, or on the root surface, depending on the nematode species. The first-stage juvenile (J1) develops inside the egg. When temperatures are favorable, the egg hatches and a second-stage juvenile (J2) emerges from the eggshell in search of a root. Once a root is found and penetrated, the nematode begins to feed and matures through two more juvenile stages (J3 and J4) before becoming an adult. Adult nematodes reproduced to generate the next generation, and depending on the nematode species, males may or may not be involved in reproduction. Different nematode species often cause similar foliar symptoms in soybean, consisting of nutrient deficiency, chlorosis, water stress, stunting, and reduced grain size. Symptom severity is dependent on the initial nematode abundance at planting, soil texture, soil water holding capacity, and susceptibility of the soybean cultivar to the nematodes.

Lance Nematode (Hoplolaimus spp.)

The lance nematode is a member of the genus Hoplolaimus von Daday (Tylenchida: Tylenchoidea). Species in this genus have a relatively broad host range that includes vegetable crops, field crops, grasses, and weed species (Fassuliotis 1974, Holguin et al. 2015). There are four species that can infect soybean: H. columbus, H. geleatus, H. magnistylus, and H. stephanus. Hoplolaimus columbus is the more damaging species on soybean, but is currently confined to the southeastern soybean-producing states. As with most plant-parasitic nematodes this species is often found in sandy soils and most active at warm (30°C or 86°F) soil temperatures (Fassuliotis et al. 1968, Fassuliotis 1975, Nyczepir and Lewis 1979). Very low initial nematode population densities of H. Columbus at planting is sufficient to cause a 10% yield loss (Noe 1993). Lance nematodes are migratory, semi-endoparasitic nematodes and feed both inside and outside of the root. Once the nematode penetrates a root, it feeds primarily on cortical cells, rarely moving beyond the endodermis and to the inner vascular cells (Fassuliotis 1975, Lewis et al. 1976). Development through the J3 and J4 stages often occur within the root system. Inside the root, a lance nematode will feed for 1–9 d, with root lesions becoming obvious after 2–3 d, causing a significant reduction in root, shoot, and pod weights (Fassuliotis 1975, Lewis et al. 1976). Eventually, females pause from feeding and move through the root tissues, commonly laying 15 or more eggs as it travels inside or outside of the root (Fassuliotis 1975). In the laboratory, lance nematodes can complete their life cycle in just 15 d, indicating that populations can increase dramatically in a single year in the field under ideal conditions (Fassuliotis 1975). Foliar symptoms consist of yellow, stunted soybean plants.

Reniform Nematode (Rotylenchulus reniformis)

The reniform nematode, Rotylenchulus reniformis Linford and Oliveira (Tylenchida: Hoplolaimidae), was first reported in the United States in 1941 in Louisiana (Smith and Taylor 1941) and since then has been detected in all major southern soybean-producing states. This nematode has a host range of over 300 plants that are mostly dicots (Heald et al. 1990, Robinson et al. 1997, Robinson 2007,
Redding et al. 2018). The reniform nematode is found in both fine and coarse-textured soils and often found at deeper soil depths than other soybean nematodes. Optimum reproduction occurs above 25°C (77°F) (Rebois 1973). The life cycle requires only 17–23 days to complete, depending on soil temperature (McGawley and Overstreet 2015). The reniform nematode is a sedentary, semi-endoparasitic nematode. The immature female is infective and penetrates the root perpendicular to the root axis. Only the anterior portion of the female is embedded in the root. The female initiates feeding by forming a feeding site, called a syncytium or nurse cell (Rebois et al. 1975, Rebois 1980). The syncytium consists of several host cells that have coalesced, resulting in a curved, multi-celled feeding site in the pericycle that serves as a nutrient source for the developing female. Once feeding is initiated, females swell into a kidney-shape, hence the name reinform, and deposit 50–75 eggs in an egg mass on the root surface (Robinson 2007). Males are often found outside of the root in the gelatinous egg mass matrix produced by embedded females. The J2 hatch from the egg and remain in the soil where they progress through juvenile stages before entering roots and starting the cycle over again. Aboveground symptoms in soybean consist of plant yellowing, stunting, and empty pods (McGawley and Overstreet 2015).

**Root-Knot Nematodes (Meloidogyne spp.)**

Root-knot nematodes are members of the genus Meloidogyne Goeldi (Tylenchida: Heteroderidae). The four most common species can all infect soybean and are *M. incognita*, *M. javanica*, *M. arenaria*, and *M. hapla* (Garcia and Rich 1985, Lima et al. 2017). The guava root-knot nematode, *Meloidogyne enterolobii* (syn. *M. mayaguensis*) is an emerging pest in the southern United States that can also infect soybean (Ye et al. 2013). These species of *Meloidogyne* all have wide and sometimes overlapping host ranges; thus, species identification is important when developing a management program. For example, neither *M. incognita* nor *M. enterolobii* reproduce on peanut (*Arachis hypogaea*), but are very successful on cotton (*Gossypium hirsutum*). On the other hand, *M. arenaria*, *M. javanica*, and *M. hapla* do not reproduce on cotton. Yet, all five species can reproduce on soybean. Of these five species, *M. incognita* is the most widely distributed and yield-limiting in the southern United States. A 75% yield loss has been reported on early-maturing soybean in a field infested with *M. incognita* (Emerson et al. 2018).

Root-knot nematode eggs survive in the soil in a gelatinous matrix, or in an egg mass inside or attached to roots. In the spring, when temperatures warm, J2 hatch, migrate to a host root, and penetrate behind the root cap. Inside the root, they migrate to the zone of differentiation and establish a feeding site in the vascular system (phloem). The J2 secrete enzymes during the feeding process that stimulate individual cells to undergo multiple divisions of the nucleus (karyokinesis) without full cell division (cytokinesis), resulting in a multinucleate, ‘giant cell’ (Mikkowski and Abawi 2003). As the J2 feeds from the giant cell, it enlarges and molts three more times through the non-feeding J3 and J4 stages to an adult. Most adult females resume feeding and enlarge, stimulating the surrounding root cells to divide and elongate to produce the diagnostic root galls or ‘knots’, as the common name implies. Root galls are the most useful diagnostic symptom, and gall size can be somewhat diagnostic of species. Root galls produced by *M. incognita* and *M. javanica* are large and irregular shaped, while those of *M. hapla* are smaller, although laboratory diagnosis is necessary for confirmation of species identity. Some species, including *M. incognita* reproduce by parthenogenesis, and eggs do not require male fertilization (Moens et al. 2009). Males are rarely observed and do not feed. Females deposit several hundred eggs in an egg mass on the root surface. Several life cycles can occur in a single cropping season, resulting in a significant increase in nematode population density in a single season. The greater the nematode population density on a susceptible soybean cultivar, the more severe symptoms will be. Foliar symptoms range from slight stunting and wilting to severe stunting, chlorosis, and premature senescence.

**Root-Lesion Nematode (Pratylenchus spp.)**

Root-lesion nematodes are members of the genus *Pratylenchus* (Tylenchida: Pratylenchidae). As their name implies, the root-lesion nematode produces lesion-like symptoms on host roots as they migrate endoparasitically through the root system. At least five *Pratylenchus* species have been reported to be parasitic on soybean: *P. brachyurus* (Godfrey) Filipjev and Schuurmans-Stekhoven, *P. agilis* Thorne and Malek (syn. *P. scribneri*), *P. alleni* Ferris, and *P. penetrans* (Cobb) Filipjev and Schuurmans-Stekhoven (Schmitt and Barker 1981). Like other plant-parasitic nematodes, lesion nematodes rarely kill their plant host, but continuously take nutrients from them (Lima et al. 2017). Root-lesion nematodes are often found in sandy soil and are most active at temperatures above 25°C (77°F) (Lewis et al. 1993), although some are capable of reproducing at temperatures as low as 15°C (59°F) (Schmitt and Barker 1981). Females lay eggs singly both inside plant roots or in the soil. Eggs may or may not require fertilization from a male depending on the nematode species (Lima et al. 2017). All life stages of the root-lesion nematode are vermiform (wormlike) and can invade and feed on root cells. As with other plant-parasitic nematodes, the root-lesion nematode uses a stylet to gain entry into root cells to feed, and lesion nematodes feed inter- and intracellularly as they migrate through the root (Lima et al. 2017). At times, root-lesion nematodes migrate out of the root and into the soil. Lesions produced by these nematodes may provide entry for other soilborne pathogens. Foliar symptoms are similar to other nematodes with unthrifty growth and chlorosis being among the most common.

**Other Soybean Nematodes**

Several species of plant-parasitic nematodes have been associated with unhealthy soybean plants (McGawley and Chapman 1983, Robbins et al. 1987, Niblack 1992), but little is known about their impact on soybean development and yield losses. Sting nematodes are members of the genus *Belonolaimus* (Tylenchida: Belonolaimidae), with *B. longicaudatus* Rau being among the best-studied and most important on soybean (*Huang and Becker 1999*). Sting nematodes are commonly found in very sandy soil (>90% sand) along the southern coastal United States (Robbins and Barker 1974). Its known geographic range is as far west as California and as far north as Delaware (Handoo et al. 2010). The sting nematode feeds on the meristem in the root tips, causing significant stunting in root development. Few studies have investigated the impact of sting nematode on soybean, but its distribution and impact on soybean and other rotation crops are of concern (Dickson and McSorley 1990, Allen et al. 2017).

Stubby-root nematodes are members of the genera *Paratrichodorus* Siddiqi (Triplonchida: Trichodoridae) and *Trichodorus* Cobb (Triplonchida: Trichodoridae). Similar to sting nematodes, stubby-root nematodes feed on the meristems in root tips, preventing normal growth and resulting in ‘stubby roots’. Roots may develop a ‘starburst’ symptom with multiple root tips expanding from a single root. Stubby-root nematodes are often found in coarse-textured soils in several of the southern soybean-producing states (Hajihassani et al. 2018), but can also be found...
in midwestern states including Iowa and Ohio (Tylka et al. 2011, Lopez-Nicora et al. 2014). Corn is very susceptible to stubby-root (Timper and Krakowsky 2006) and may exacerbate a stubby-root nematode problem. The stubby-root nematode can also vector plant viruses, although the impact of this on soybean production is currently unknown (Decraemer 1991). Additional nematodes are known to reproduce on soybean, but their economic impact is minimal or unknown.

Genetic Resistance
Genetic resistance to nematodes is a desirable and cost-effective management tool. As a general rule, genetic resistance to nematodes is often species or genera specific. For example, soybean cyst nematode-resistant cultivars are susceptible to root-root-knot nematodes and vice-versa (Davis et al. 1996). There is an apparent correlation with resistance to soybean cyst nematode and the reniform nematode (Rebois et al. 1970), but a shared resistance mechanism in soybean has not been identified (Kim et al. 2016). Soybean resistance to M. incognita is available in many cultivars (Emerson et al. 2018), but this resistance is not effective against other Meloidogyne species. There is no reported resistance to root-lesion, sting, lance, or stubby-root nematodes in soybean.

Several studies have identified varying magnitudes of tolerance to the lance nematode in soybean (Nyczepir and Lewis 1979, Schmitt and Imbriani 1987, Mueller et al. 1988). Although these cultivars may tolerate lance nematode feeding, they do not suppress the nematode population density for future crops.

Several soybean cultivars have resistance to reniform nema- todes (Robbins et al. 1999), some with strong enough genetic resistance to be useful in crop rotations with other susceptible crops like cotton (Gilman et al. 1978, Davis et al. 2003, Koenning et al. 2004). However, relying solely on genetic resistance for nematode management can promote nematode selection towards overcoming the resistance, diminishing the effectiveness of genetic resistance in nematode control, as seen with soybean cyst nematode. With both reniform and root-knot nematodes, earlier-maturing cultivars tend to lack genetic resistance (Robbins et al. 1999, Emerson et al. 2018), so soybeans grown in northern states may lack effective levels of genetic resistance to these nematodes. If warming temperatures continue on their current trends, non-soybean cyst nematode nematodes could become more common and damaging in northern states that plant earlier-maturing cultivars.

Crop Rotation
Crop rotation options are specific to individual soybean nematodes, thus knowing which species are present in a field is vital. Ideally, a non-host crop is the best option, but adopting a new crop into a rotation sequence can be limited by soil type, market availability, and cost of new equipment (Rodriguez-Kabana et al. 1988). Examples of non-host crops for M. incognita management that are being used are peanut and sesame (Sesame indicum) (Starr and Black 1995). However, both have significant drawbacks in rotation with soybean. Peanuts, like soybeans, are legumes, so they share several diseases with soybean. Peanut also requires unique equipment for harvest and are not well-adapted to much of the northern Midwest. Sesame has not been as widely adopted in crop rotations because it is not as profitable as other rotational crop options. Corn or grain sorghum are considered non-host crops for the reniform nematode and have been used effectively, although the profitability of grain sorghum varies from year to year. A dry fallow rotation can also be helpful for managing some plant-parasitic nematodes, but the recommended duration of the fallow may be impractical. For example, the reniform nematode can withstand dry conditions for several years, then rehydrate and infect a host crop (Sehgal and Gaur 1988, Santini et al. 2004). As mentioned above, the soybean cyst nematode can survive 10 yr or more in the absence of soybean. Due to the wide host range of the root-lesion nematodes, there are few options for crop rotation (Lima et al. 2017). Corn hybrids vary in their susceptibility and root-lesion nematode can survive at least 90 d in dry soil, so a fallow rotation may not help either (Neves et al. 2012). The lance nematode has a broad host range that includes common crops including corn, cotton, and soybean; however, peanut, tobacco, and small grains are poor hosts to this species of lance nematode and may provide some help in rotation with soybean (Subbotin and Chitimbar 2018).

Ectoparasitic nematodes also have broad host ranges with few poor hosts. Corn, sorghum, and wheat rotations with soybean failed to reduce sting nematode populations, but rotations with alfalfa lowered sting nematode population densities (Todd 1991). Similarly, wheat, oat, and rye rotations with soybean failed to reduce stubby-root nematode numbers (Minton and Bondari 1994), but tall fescue was effective in lowering stubby-root nematode population densities (Pederson et al. 1988).

Chemical and Biological Control
Due to the scarcity of efficient and economically attractive crop rotation options, nematicides are commonly integrated into nematode management in soybean. Fumigant nematicides have a long history of use in successful nematode management (Minton et al. 1980, 1985; Rodriguez-Kabana et al. 1982; Schmitt and Bailey 1990; Minton and Bondari 1994; Barker and Koenning 1998). However, chemical fumigants are not being used due to negative effects reported on beneficial microbes (Nyczepir and Lewis 1979) and negative environmental impacts (Gowen 1997). Non-fumigant nematicides such as aldicarb, carbofuran, and fenamiphos have also been historically used for successful nematode management (Mueller and Sanders 1987, Schmitt and Imbriani 1987, Schmitt and Bailey 1990). Due to similar environmental and off-target concerns as fumigant nematicides, the use of these nematicides has been vastly reduced and is under strict regulation of the Environmental Protection Agency (Oka et al. 2000, EPA 2010).

During the past decade, new nematicides have been approved for use in soybean. These products have more specific modes of action and lower environmental impacts than fumigant and non-fumigant predecessors in the past (Schmitt and Imbriani 1987, Faske and Hurd 2015, Jeschke 2015, Kandel et al. 2017, Beeman and Tylka 2018, Beeman et al. 2019, Roth et al. 2020). Identifying other novel nematicides continues to be an active area of research among agricultural chemical companies (Jeschke 2015).

Grasses like tall fescue are known to harbor fungal endophytes. Tall fescue was reported to reduce stubby-root nematode densities (Pederson et al. 1988), root-knot nematode reproduction (Elmi et al. 2000, Nyczepir and Meyer 2010), and root-lesion nema- tode reproduction (Bernard and Gwinn 1991), which is attributed to the presence of endophytic fungi that produce compounds that deter nematodes and other insect herbivores (Breen 1994). Other fungal isolates from many genera have recently been investigated for their control of plant–parasitic nematodes in soybean fields (Strom et al. 2020, Haarith et al. 2020). Agricultural companies are also investigating biological control and marketing biological nematicides. Commercially available bio-nematicides are most commonly applied as seed treatments and currently outnumber chemical nematicides that are registered for use on soybean.
Tillage
Tillage affects larger soil organisms more than smaller organisms (Kladivko 2001). Although tillage can theoretically be beneficial in nematode-infested fields, historically the impact on nematode population densities are variable (Minton 1986), and different tillage practices affect different nematodes differently (Barker and Koening 1998). More recent studies continue to find different effects of tillage on different nematodes, such as minimum tillage reducing soybean cyst nematode and lesion nematodes, but having no effect on spiral nematodes (Grabau et al. 2017).

Frogeye Leaf Spot
Introduction, Impact, and Disease Cycle
Frogeye leaf spot of soybean is caused by the fungus Cercospora sojina K. Hara (Cannadiales: Mycosphaerellaceae), which can be found worldwide (Athow and Probst 1952, Bernaux 1979, Akem et al. 1992, Ma 1994). First identified in Japan in the early 1900s, C. sojina was soon found in the United States (Melchers 1925, Lehman 1928). Frogeye leaf spot was first recognized as a disease predominantly in the southern United States, but the incidence in northern regions has become more frequent (Athow and Probst 1952, Yang et al. 2001, Mengistu et al. 2002, Grau et al. 2004). Although it is unclear why the pathogen has increased in incidence in the north, it is possible that it could be surviving due to warmer winter temperatures as a result of climate change or increased crop residue as a result of commonly adopted no-till practices (Mian et al. 2008). Between 2010 and 2014, frogeye leaf spot ranked in the top 10 yield-limiting diseases in 4 out of the 5 yr. Estimated losses due to the disease ranged from 100,000 to 493,000 tonnes (3.7 to 18.1 million bushels) per year (Allen et al. 2017).

The fungus survives the winter as mycelium in crop residue and in infected seed (Singh and Sinclair 1985). Discoloration of the seed is associated with infection, and greater discoloration is associated with lower germination (Sherwin and Kreitlow 1952, Wise and Newman 2015). If the infected seed is able to germinate, the resulting seedling will often be stunted and exhibit lesions developing on the cotyledons. Spores may develop on infected cotyledons and serve as inoculum for infecting leaves of nearby plants. Lesions will begin to develop 1–2 wk after the initial infection. Once lesions are present, conidia can be produced within 48 h under humid conditions. Conidia are then dispersed by wind or splashing rain to infect surrounding leaves and plants. Young leaves are typically most susceptible to new infections. Infections on mature leaves develop smaller, less damaging lesions. Lesions are also capable of developing on stems and pods, potentially leading to diseased seeds. Under conducive environments, including high temperatures, high humidity, and frequent rainfall or irrigation events, this disease is polycyclic, leading to large portions of fields being affected throughout the course of a season.

Genetic Resistance
The use of resistant cultivars was very effective for managing frogeye leaf spot disease in the United States until the late 1950s when C. sojina race 2 emerged (Athow et al. 1962). This was followed by the appearance of races 3 and 4 in North Carolina during the 1960s (Ross 1968) and race 5 in 1978 (Phillips and Boerma 1981). Currently, 11 races of C. sojina have been identified, suggesting a wider genetic diversity than previously believed (Mian et al. 2008). Due to the number of races currently known to exist, host resistance genes may not be effective in reducing disease against all races. Therefore, it is important to incorporate multiple resistance genes into cultivars for greater disease control. Currently, there are three resistance genes (Rcs1, Rcs2, and Rcs3) that confer resistance to economically important races of C. sojina within the United States, although each gene reacts differently to each race. Rcs1 confers resistance to race 1, Rcs2 confers resistance to race 2, and Rcs3 confers resistance to all known races in the United States (Athow and Probst 1952, Probst and Athow 1958, Athow et al. 1962, Probst et al. 1965, Phillips and Boerma 1981, Boerma and Phillips 1983, Mian et al. 1999, Missaoui et al. 2007). Although these genes were discovered over 30 yr ago, Zhang and Bradley (2017) report that the Rcs3 gene was still effective in conferring resistance to modern isolates of C. sojina. While other distinct resistance genes have been identified, they do not confer resistance to the economically damaging races found in the United States (Face et al. 1993, Baker et al. 1999, Pham et al. 2015). Genetic resistance is a critically important tool used for managing frogeye leaf spot. Because of the potential for resistance breakdown, other control methods should also be integrated with genetic resistance.

Crop Rotation and Tillage
There are no reports of any alternative hosts of C. sojina, suggesting that crop rotations with other crops like corn, alfalfa, or small grains could help decrease the survival of the pathogen. If the disease has been severe in certain fields, long crop rotations for many years might be necessary to evade a reemerging disease risk (Zhang and Bradley 2014, Bradley et al. 2016). Tillage may allow for quicker or more complete breakdown of crop residue and a reduction in C. sojina survival (Bradley et al. 2016).

Chemical and Biological Control
Foliar fungicides have shown efficacy in controlling frogeye leaf spot and protecting yield when applied between the R1 and R5 growth stages (Akem 1995). Cercospora sojina isolates resistant to QoI fungicides were first reported in the United States in 2010 in Tennessee (Zhang et al. 2012), and have since been reported to occur in 15 additional states to date (Standish et al. 2015, Zeng et al. 2015, Zhang et al. 2018, Mathew et al. 2019). Fungicide active ingredients other than the QoIs must be utilized for effective fungicide control of frogeye leaf spot. Foliar fungicide applications reduced frogeye leaf spot disease severity and increased yields in conventionally tilled fields but not in no-till operations, suggesting that cultural practices may interact with foliar fungicide applications (Mengistu et al. 2014). The impact of tillage on disease incidence and severity should be explored more fully. The strains of Bacillus amyloliquefaciens, BNM340 and BNM122, have been suggested as a biological means of control of C. sojina. When applied to the foliage of seedlings, disease severity was lower than where they were not applied (Simonetti et al. 2012).

Diaporthe Diseases
Introduction, Impact, and Disease Cycles
Soybean is affected by fungi within the Diaporthe (syn. Phomopsis) Sacc. & Roum. (Diaporthales: Diaporthaceae) genus. Diseases include pod and stem blight (Diaporthe sojae, D. gulyae), Phomopsis seed decay (D. longicolla), and Northern and Southern stem canker (D. caulivora and D. aspalathi, respectively). Estimated yield losses due to Diaporthe diseases between the years of 2010 and 2014 ranged from 400,000 to 993,000 tonnes (14.7 to 36.5 million bushels) (Allen et al. 2017). Pod and stem blight is most common on mature plants and can result in premature death and infection of seed. Stem canker can also result in premature death of plants...
reported to lead to losses up to 50% in heavily infested fields planted with susceptible cultivars (Wise et al. 2015). Phomopsis seed decay is the leading cause of low seed quality in soybean production areas because it reduces seed oil content, lowers viability, and increases incidence of moldy or split seeds (Hepperley and Sinclair 1978, Rupe and Ferriss 1986, Rupe 1990, Sinclair 1993, Meriles et al. 2004). The development of these diseases is favored by hot and wet conditions, especially late in the season when the crop is drying down (Shourt et al. 1981, Balducchi and McGee 1987).

*Diaporthe sojae* and *D. longicolla* persist in contaminated seed or on old crop residue. Primary infections can be the direct result of planting infected seed, or plants can become infected during the growing season when asexual (pycnidia) and sexual (perithecia) fruiting bodies, produced on infested crop residue produce asexual and sexual spores (Hildebrand 1956). These spores are deposited onto leaf tissue by rain splash, and germination occurs if leaf wetness is maintained for several hours (Athow and Caldwell 1954). The fungi are only capable of growing within 5 cm (2 inches) of the initial infection point. Damaged or senescing leaves are most susceptible to the fungal pathogens and will exhibit greater disease symptoms. Further production of spores allows for secondary spread of disease throughout the season. Infections on pods can result in infected seed and seed decay. For this to occur, infection on pods must take place around the R5-R6 growth stages, with symptoms appearing on maturing pods and seeds at or past the R7 growth stage (McGee 1986). Infected seeds can range from being symptomless to being severely shriveled and cracked, or white and chalky.

Both *D. caulivora* and *D. aspalathi*, causal agents of stem canker, overwinter in crop residue and can also be introduced to a field by planting infected seed. Seed transmission of *D. aspalathi* is typically less than 1%, while seed transmission rates for *D. caulivora* can reach 10–20% (Rupe 2015). Considerably more epidemiological work has been done on southern stem canker (caused by *D. aspalathi*), but it is likely that northern stem canker (caused by *D. caulivora*) behaves in a similar manner. When conditions are warm (>20°C) and wet, sporulation on crop residue occurs, and spores are splashed to plants by rain. Leaf wetness must be maintained for 24–96 h and temperatures must be between 22 and 30°C for spores to germinate and infect host tissue (Rupe 2015). After infection occurs, the fungus is capable of fully girdling the stem and restricting vascular flow, leading to sudden and premature plant death. Leaves may also exhibit interveinal yellowing and senescence while remaining attached to the plant. Damage caused by *Diaporthe* spp. is expected to increase and incidence may expand as the climate becomes warmer and wetter (Bebber et al. 2013).

### Genetic Resistance

The use of genetic resistance is the most effective control method for both northern and southern stem canker diseases (Weaver et al. 1984). Many cultivars have been released spanning multiple maturity groups and exhibiting varying levels of resistance (Kilen et al. 1985; Brown et al. 1987; Li 2011; Li et al. 2011, 2015, 2017b). Resistance genes to Phomopsis seed decay have also been identified and show promise in the future cultivars (Zimmerman and Minor 1993; Smith et al. 2008; Jackson et al. 2005, 2009). One resistance gene found in the plant introduction PI80837 has been mapped to molecular linkage group B2 on chromosome 14 (Jacksen et al. 2009). Additional genes have been identified that control the resistant response in a dominant mode of inheritance (Kilen et al. 1985). These genetic characterizations allow for the use of marker-assisted selection for increased speed and precision in breeding programs.

### Crop Rotation

Crop rotation with corn or small grain crops is recommended for managing both northern and southern stem canker, because they are effective at reducing levels of inoculum for future years (Li et al. 2015). Unfortunately, cotton, a common crop in the southern United States, is a host for *Diaporthe* spp., limiting the effectiveness of rotations involving cotton (Roy and Miller 1983). There are few alternative hosts for *D. caulivora* and *D. aspalathi*, but other common economic crops have not been studied extensively as rotation crop options.

### Chemical Control

The use of fungicide seed treatments is essential for managing seed decay and maintaining high germination rates, and seed treatments should be used if the level of *Phomopsis* seed infection is greater than 15% (Kmetz et al. 1978, Hobbs et al. 1985, Li et al. 2015). Fungicide treatment of *Diaporthe*-infected seed resulted in increased seedling emergence and yield (Xue et al. 2007). The use of fungicide seed treatments in conjunction with biological agents *Bradyrhizobium japonicum* and *Clonostachys rosea*, may increase the effectiveness of control (Xue et al. 2007).

Certain foliar fungicides have been shown to be efficacious for decreasing *Phomopsis* spp. disease incidence. Applications of pyraclostrobin and tebuconazole between R3 and R5 growth stages resulted in decreased stem and seed infection by *Phomopsis* spp. (Soto-Arias and Munkvold 2011). Conversely, applications of QoI fungicides or a combination of QoI and SDHI fungicide showed similar or increased levels of *Phomopsis* spp. in seed compared to the non-treated control or where a benzimidazole fungicide was used (Wreather et al. 2004, Batzer and Mueller 2020). Although the mechanisms for this increase is not known, it may have been potentially due to impacts on the endophytic communities on the aboveground soybean plant parts by the fungicides (Batzer and Mueller 2020). Foliar fungicide applications were also found to increase yields in cultivars susceptible to stem canker, but no yield benefit was seen in resistant cultivars (Backman et al. 1985). It is likely that optimal timing of foliar fungicide applications to control *Diaporthe* diseases will depend on both the abundance of seedborne inoculum and in-season weather trends.

### Cultural Control

Ensuring seed is clean and not infected prior to planting, especially in fields that have had no history of disease is a very effective method of reducing disease incidence. In addition to introducing the pathogen into new areas, planting infected seed can also result in damping-off and decreased plant stands (Sinclair 1993). It is also important to clean all equipment when moving from an infested field to a non-infested field, so new inoculum is not introduced. Plant stress by either drought or nematodes is known to be related to increased disease severity, so timely and proper irrigation and effective nematode management are both important in lowering the incidence and severity of disease (Backman et al. 1985). Harvesting soybeans should also be done in a timely manner, reducing the risk that the crop is exposed to adverse weather conditions late in the season, increasing the development of seed decay.

Due to the importance of crop residue for successful pathogen overwintering, tillage can be used to reduce disease by increasing the rate of residue decomposition. No-till practices have been shown to result in higher incidence of stem canker due to retention of residue on the soil surface for the pathogen to survive (Tyler et al. 1983).
Soybean is the second most plentiful crop in the U.S. Farmers plant over 39.6 million hectares (98 million acres) of soybeans each year, second only to field corn (USDA Farm Service Agency 2019). Because soybean is such a large component of the U.S. agricultural economy, protection of the crop against consistent, intermittent, and emerging diseases are of major economic importance. This review covers the known yield-limiting diseases affecting soybean production in the United States.

If temperatures continue to increase as predicted, causal agents such as the charcoal rot and frogeye leaf spot pathogens may be capable of surviving winters in more northern soybean growing regions. Similarly, increased soil temperatures may also provide a more favorable environment for many plant-parasitic nematodes. As precipitation levels increase, Diaporthe diseases and Phytophthora root and stem rot could increase in incidence throughout the growing region. This increase in temperature could also change the traditional range of some of these diseases, or actually lower incidence or severity. For example, increasing temperatures could lead to decreased apothecial germination and infection of soybean by the Sclerotinia stem rot pathogen, S. sclerotiorum, in its current geographic range. Prediction models suggest the increasing abundance of plant pathogens globally, which has so far been supported by the correlation of pathogen presence and warming conditions (Delgado-Baquerizo et al. 2020). Overall increasing temperature and precipitation will likely favor greater pressure from other agronomic pests, including weeds and insects, as well as pathogens and nematodes. Increased insect vector pressure could increase the incidence and economic importance of certain soybean viruses. Additionally, the effects that these weather events may have on other factors, such as genetic resistance or chemical efficacy, remain unknown.

Future demand for food and fiber will no doubt increase in the coming years as the world population continues to expand. It has been predicted that global food production must increase between 60 and 100% by 2050 simply to maintain growing populations (Tilman et al. 2011, Alexandratos and Bruinsma 2012). Estimates on the global burden of plant diseases suggest that the impact of yield losses will be most severe in food-deprived regions (Savary et al. 2019). Efforts to increase crop production has largely focused on increasing yields in the past 20 yr, although recently more attention has been put on decreasing crop losses and reducing food waste (Savary et al. 2017). More focus is needed on developing disease prediction tools that can be used to anticipate in-season threats and project future outbreaks. These tools can be used in long-term decision making to better anticipate emerging disease issues so that management practices can be tailored appropriately. Two avenues that will be vital for meeting the increased demand for agricultural products: 1) We must be able to anticipate significant disease outbreaks and protect crops effectively from pathogens, and 2) we must continue to emphasize yield gains through genetic disease resistance. It is crucially important to understand the major diseases of soybean and those that are emerging so that we may be prepared for the challenges of the future.

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