


Determination of weed hosts of soybean cyst nematode in South Dakota

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Research Article

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Canada thistle, *Cirsium arvense* (L.) Scop.; common cocklebur, *Xanthium strumarium* L.; common mallow, *Malva neglecta* Mallr.; field pennycress, *Thlaspi arvense* L.; purple deadnettle, *Lamium purpureum* L.; shepherd's purse, *Capsella bursa-pastoris* (L.) Medik.; white clover, *Trifolium repens* L.; soybean, *Glycine max* (L.) Merr.; soybean cyst nematode, *Heterodera glycines* Ichinohe

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Abstract

Soybean cyst nematode (SCN) causes over \$1.2 billion in revenue loss annually in the United States and consistently ranks as the most threatening pathogen for soybean. SCN weed hosts have been documented in other states in the eastern Corn Belt, but very little work has been done in the midwestern Corn Belt. To determine alternative SCN weed hosts in South Dakota, 670 whole weed root samples comprising 63 weed species were collected from 48 SCN-positive fields in 13 counties during fall 2016 and spring 2017. Among the 63 weed species, 12 contained SCN juveniles and 7 were confirmed hosts of SCN based on the completion of the SCN life cycle in greenhouse studies. Ranking of female index (FI) for the weed hosts were purple deadnettle (FI = 34.6) > field pennycress (FI = 26.9) > common mallow (FI = 2.04) > shepherd's purse (FI = 1.89) > white clover (FI = 1.86) > Canada thistle (FI = 1.24) > common cocklebur (FI = 1.10). These results indicate that some weeds can support SCN, and therefore a proactive weed management approach should be employed for fields infested with SCN.

Introduction

Soybean is the second most important crop after corn in South Dakota, with acreage of 2.3 million hectares and generating close to \$2.2 billion in revenue (USDA-NASS 2018). However, its production in South Dakota is threatened by the soybean cyst nematode (SCN) (Allen et al. 2017; Niblack et al. 2006). SCN has been reported in 31 counties of South Dakota (Acharya 2015; Tylka and Marett 2017), and this pest is continuously spreading to other areas in the state. The estimated soybean yield loss due to SCN in South Dakota alone is 120 million kg annually (www.sdsoybean.org) and is expected to increase if efforts to minimize its spread are unsuccessful.

Soybean cyst nematode is a soilborne, obligatory, sedentary, endoparasitic nematode that parasitizes soybean roots (Niblack et al. 2006). Not only does feeding of SCN on soybean roots reduce nutrients for the plant, but wounds created by juveniles can be entry routes for other pathogens such as *Fusarium virguliforme* (Workneh et al. 1999). SCN belongs to phylum Nematoda, order Tylenchida, and family Heteroderidae. The genus *Heterodera* comprises cyst-forming nematodes that are characterized by their ability to form cysts (thick-walled female body that is filled with eggs) that provide overwintering protection for eggs (Davis and Tylka, 2000).

The SCN life cycle comprises three main stages: egg, juvenile, and adult. The egg goes through different phases of embryogenesis and molting, resulting in the formation of the first-stage juvenile (J1) inside the egg (Niblack 2005). The J1s molt into a second-stage juvenile (J2), which is the infecting stage. The J2s are attracted to the roots by root exudates and enter the host's roots with the aid of a stylet (penetrating organ), finally migrating toward the vascular system of the plant. The juvenile destroys cortical and epidermal cells to form a metabolic sink often referred to as a syncytium (Davis et al. 2004). Juveniles feed from the syncytium and become sedentary, undergoing further molt into the third-stage juvenile (J3), where the sexual differentiation occurs. J3 males undergo metamorphosis, regaining their vermiform shape, whereas J3 females continue to feed and eventually change into a lemon-shaped cyst. SCN takes around 3 to 4 wk to complete its life cycle, but the duration is influenced by several environmental and genetic factors (Riggs and Wrather 1992).

Use of SCN-resistant soybean cultivars and crop rotations with non-host crops are commonly practiced techniques for SCN management (Mitchum 2016; Niblack and Chen 2004). However, the majority of host resistance used in SCN management was derived from one source (PI88788), and several reports indicate adapted SCN populations that can reproduce well on this resistance source (Gardner et al. 2017; Howland et al. 2018; Tylka and Mullaney 2018; Zheng and Chen 2011). Another challenge associated with use of host resistance is that some of the

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farmers are not adopting SCN-resistant varieties because they have not tested their soils to determine presence of SCN. SCN does not cause obvious aboveground symptoms when the SCN population density is low, though by this time yield loss is already occurring (Wang et al. 2003).

Weed SCN hosts further complicate SCN management because of continued SCN development in the soil in the absence of soybean (Creech et al. 2005; Johnson et al. 2008; Nice and Johnson 2005; Poromarto et al. 2015; Thomas et al. 2005). Winter annual weeds emerge during fall, overwinter as seedlings, and then complete their life cycle in the spring (Mock et al. 2007; Werle et al. 2014). Previous studies have shown that there has been a surge in the winter annual weeds in different states that is probably due to factors such as increased conservation tillage practices, herbicide usage for weed management, and warmer winters in northern US regions (Johnson et al. 2008; Krausz et al. 2003; Thomas et al. 2004).

SCN reproducing on the alternative weed hosts may also influence the HG type (*Heterodera glycines* type) as a result of selection pressure favoring development of a particular SCN HG type (Niblack 2005). HG type is a modified classification system of SCN by considering the relative reproduction of SCN on seven soybean differential lines as compared to the standard susceptible check (Niblack et al. 2002; Wang et al. 2013). An SCN population is determined to be virulent to the specific differential line if the relative number of cysts developed on this line is $\geq 10\%$ of the number of cysts that developed on a susceptible line. Acharya et al. (2017) reported diverse HG types in South Dakota counties, and this can be attributed in part to weed hosts in soybean fields. It is therefore important to identify weeds that are hosts for SCN in South Dakota so as to inform SCN management approaches.

Some commonly found weed hosts of SCN documented in several soybean-producing US states of Indiana, Ohio, Illinois, North Dakota, Iowa, and Missouri include burclover (*Medicago polymorpha* L.), alsike clover (*Trifolium hybridum* L.), crimson clover (*Trifolium incarnatum* L.), common chickweed (*Stellaria media* L. Vill.), mouse-ear chickweed (*Cerastium fontanum* Baumg.), common mullein (*Verbascum thapsus* L.), field pennycress or henbit (*Lamium amplexicaule* L.), and purple deadnettle (Chen 2012; Giesler and Wilson 2011; Mock et al. 2007; Poromarto et al. 2015; Tylka 2012; Werle et al. 2015). However, identification of SCN weed host species is complicated because of the genetic variability of HG types, localized environment, and selection pressure associated with different agronomic practices (Riggs and Schmitt 1988). The considerable temperature dependence of SCN growth and development influences their success on winter annual weeds (Creech et al. 2007).

Despite the importance of weeds as alternative hosts to SCN, no information is available on weeds that are SCN hosts in South Dakota. South Dakota has diverse cropping systems including no-tillage or minimum tillage, which influences the weed species present, some of which may be hosts of SCN. Moreover, only a few research studies on weeds as SCN hosts have included field-based information. Creech and Johnson (2006) reported on abundance of broadleaf winter weeds in fields infested with SCN in Indiana but did not report on the SCN reproduction on these weed hosts. Mock et al. (2012) studied the influence of winter annual weed management and crop rotation on SCN. However, individual weed support of SCN reproduction was not reported in their study. Although

Creech et al. (2005) reported SCN reproduction on weed hosts based on field conditions, they investigated only two weed hosts. Moreover, weed diversity and abundance in the above study locations are different from South Dakota, which is located in the northern plains.

Most of the reports on SCN weed hosts done in several states had contrasting reports of plant species determined to be SCN hosts that were mainly due to different biotypes of the weed species tested (Poromarto et al. 2015). Hence, it is important not only to identify state-specific weed hosts due to agronomic and abiotic differences among states, but also to test host status under field and greenhouse conditions. Therefore, the objective of this study was to determine weeds that host SCN based on field conditions supplemented with further greenhouse testing.

Materials and Methods

Weed Sample Collection

Previously confirmed SCN-positive fields (Acharya 2015) in 13 different soybean-growing South Dakota counties were identified arbitrarily. Weed samples were collected from 48 fields selected at random in the fall of 2016 from September to November (11 fields) and in the spring of 2017 in late April and May (37 fields). Sampling in the fall targeted weeds that emerge after soybean harvest, whereas the spring sampling targeted weeds that emerge before soybean planting. Temperature ranges for September to November and for April through May for eastern South Dakota in 2016 and 2017 were within the 30-yr averages of -7°C to 26°C for September through November and 0°C to 23°C for April and May (NWS 2018). For each field, whole weed samples were collected from locations likely to have SCN within the field including field entrances and low-lying areas. For each weed sample, the whole weed with its soil ball from a depth of 30 cm was obtained. At least two samples for each weed species were collected in each field. Samples were placed in plastic bags and stored in a cooler (4°C) until SCN extraction (within a week). Additionally, soil samples of approximately 2 to 3 kg were collected from every sampled field in a zig-zag pattern to confirm the presence of SCN through a standardized soil-washing extraction procedure as described below.

SCN Extraction

SCN cysts and eggs were extracted from 100 cm^3 of the representative soil sample following the extraction procedures by Faghihi and Ferris (2000). SCN extraction was done within a week of sampling for weed samples and within a month for the soil samples. Of 48 fields positive for SCN, 45 were used for further weed SCN hosts analysis. The root ball of the weed samples was placed in a bucket filled with water and left to soak for 48 h to facilitate removal of soil from the roots. Roots were cut into small pieces (length 1 to 2 cm) and macerated in a blender with 100 ml water at 12,000 rev/min for 1 min (EPPO 2013). The resulting suspension was passed through two sieves with a $250\text{-}\mu\text{m}$ sieve above a $25\text{-}\mu\text{m}$ sieve at the bottom. The suspension from the $25\text{-}\mu\text{m}$ sieve was collected in a 50-ml beaker, and a 1-ml aliquot was transferred to a counting slide and analyzed for the presence of juveniles using a dissecting microscope (Faghihi and Ferris 2000). Juveniles of SCN were identified based on morphology (Hunt and Lane, 2008) and enumerated.

Greenhouse Assay to Confirm Weeds as SCN Hosts

The greenhouse experiment examined the cyst development in weed species that tested positive for SCN as described above. The weed species included field pennycress, purple deadnettle, white clover, common mallow, Venice mallow (*Hibiscus trionum* L.), purple poppy mallow [*Callirhoe involucrata* (Torr. & A. Gray) A. Gray], horseweed (*Erigeron canadensis* L.), shepherd's purse, common cocklebur, Canada thistle, small-flowered bittercress (*Cardamine parviflora* L.), and leafy spurge (*Euphorbia esula* L.). Weed seeds of these species (except small-flowered bittercress) were pre-germinated at room temperature (25°C) in a Petri dish with a moist filter paper. Pre-germinated seeds of each weed species and susceptible soybean cultivar Williams 82 as the susceptible check were transplanted into individual cone-tainers (3.8 cm diam and 21 cm height; Stuewe and Sons Inc., Tangent, OR) filled with sterilized clay-sand mixture (1 part clay to 2 parts sand). Each cone-tainer was planted with a single pre-germinated seedling. Each cone-tainer was inoculated 3 cm below the soil surface by pipetting a 1-ml aliquot of water containing 2,000 SCN eggs (HG type 0) per milliliter into the soil 3 d after transplanting. HG type 0 was used because it is the most predominant HG type in South Dakota (Acharya et al. 2016). The cone-tainers were placed in a 7.6-L bucket filled with sand and placed in a water bath maintained at 27 C to 28 C (ideal temperature for SCN reproduction; Palmateer et al. 2000). Each bucket contained one replicate of each weed species and a susceptible check.

The hatching rate of HG type 0 eggs was 50% within 10 d. The weed species with the susceptible soybean check were arranged in a completely randomized design with eight replicates, and the whole experiment was repeated once.

After 40 d post-inoculation, the cone-tainers were removed from the bucket and soaked in water for 20 min. The plants were then uprooted. The 40-d duration was chosen to provide enough time for life cycle completion on weed species under greenhouse conditions. A strong stream of water was applied on the roots to dislodge cysts, which were collected on a 210- μ m sieve nested under a 710- μ m sieve. The total number of cysts that developed on the root were counted and used to calculate the female index (FI):

$$FI = \frac{\text{Average number of cysts found on the weed species}}{\text{Average number of cysts found on the susceptible check}} \times 100$$

FI is the relative measure of SCN reproduction on a plant species as compared to a standard susceptible soybean check and is a preferred measure to determine the reproduction capacity of SCN on a given species (Niblack et al. 2002).

Data Collection and Summary

The weed field prevalence was determined as frequency obtained by dividing the number of fields found with the weed species by the total fields scouted. The average number of SCN eggs found in a county was determined by dividing the sum total of eggs in the soil samples by the number of soil samples obtained in a county. Average number of SCN juveniles in weed roots was obtained by dividing the sum of the juveniles extracted from weed roots by the number of root samples used for extraction for each weed species. Number of cysts that developed on each weed species

and respective FI for each weed species were averaged across replications and runs. Because data collected were frequencies and no treatments were imposed, no statistical tests were necessary and discussion of the data was done by comparing percentages.

Results and Discussion

Of 670 whole weed samples collected from the fields during fall 2016 and spring 2017, Canada thistle was the most abundant, with a distribution frequency of 69% (33 of 48 fields sampled) (Table 1). Other commonly found weeds included common lambsquarters (*Chenopodium album* L.) (59%), field pennycress (56%), dandelion [*Taraxacum officinale* (L.) Weber ex F.H. Wigg.] (50%), white clover (46%), field bindweed (*Convolvulus arvensis* L.) (44%), common cocklebur (42%), and Kochia [*Bassia scoparia* (L.) A.J. Scott] (42%) (Table 1). Weeds such as alfalfa (*Medicago sativa* L.), small-flowered bittercress, black-seeded plantain (*Plantago rugelii* Decne), common chickweed, field horsetail (*Equisetum* spp.), moth mullein (*Verbascum blattaria* L.), musk mallow (*Malva moschata* L.), purple poppy mallow, prostrate knotweed (*Polygonum aviculare* L.), wild onion (*Allium ascalonicum* L.), and yellow spine thistle (*Cirsium ochrocentrum* A. Gray) were collected in <3% of the fields sampled.

SCN was not detected in bulk soil samples collected in 3 of the 48 fields, and weed roots from these fields were not tested for SCN. SCN populations from the 45 SCN-positive fields ranged from 700 to 100,000 eggs per 100-cm³ soil sample, suggesting highly variable SCN populations in the infected fields in South Dakota (Table 2). In general, SCN population within and across locations is influenced by several biotic, abiotic, and agronomic factors. Some of the abiotic factors affecting SCN are soil temperature, soil characteristics, soil moisture content, salt content, pH, and metal ions. Biotic factors include presence of microorganisms, plant exudates, and weeds. Agronomic factors such as tillage, soil nutrients, nematicide seed treatments, and cropping history also affect SCN level (Gavassoni et al. 2007; Workneh et al. 1999).

Among all the weed species, a comparatively higher number of SCN juveniles (>15) were obtained from purple deadnettle, Venice mallow, white clover, and field pennycress (Table 3). Fewer juveniles (1 to 3) were found from common cocklebur, common mallow, horseweed, small-flowered bittercress, shepherd's purse, Canada thistle, leafy spurge, and purple poppy mallow (Table 3). There was no correlation between soil SCN population density and number of juveniles found in weed species. Similarly, time of sampling did not influence the weed species or juvenile densities found in roots (data not shown). Juveniles determined from field weed species were relatively fewer (1 to 20) compared to SCN egg counts, which ranged from 700 to 4,050 eggs per 100 cm³ of soil. The lack of correlation between juveniles in weed species roots and egg count in the soil samples within the same field might be due to SCN weed host preferences and high SCN variability within the field. High SCN within-field variability can be caused by several factors such as field landscape, soil type, tillage practices, and soil moisture (Gavassoni et al. 2007; Perez-Hernandez and Giesler 2017; Workneh et al. 1999). Although the HG type for each individual sampled field was not determined in this study, a previous

Table 1. Collection frequency (%) of weed species obtained from the field survey ($n = 48$) to determine weed hosts for soybean cyst nematode in South Dakota during the fall of 2016 and spring of 2017.

Weed species	Scientific name	Field frequency %
Canada thistle	<i>Cirsium arvense</i>	69.4
Common lambsquarters	<i>Chenopodium album</i>	58.9
Field pennycress	<i>Thlaspi arvense</i>	56.8
Dandelion	<i>Taraxacum officinale</i>	50.5
White clover	<i>Trifolium repens</i>	46.3
Field bindweed	<i>Convolvulus arvensis</i>	44.2
Common cocklebur	<i>Xanthium strumarium</i>	42.1
Kochia	<i>Bassia scoparia</i>	42.1
Horseweed	<i>Erigeron canadensis</i>	37.9
Curly dock	<i>Rumex crispus</i>	37.9
Prostrate knotweed	<i>Polygonum aviculare</i>	35.8
Common ragweed	<i>Ambrosia artemisiifolia</i>	35.8
Common milkweed	<i>Asclepias syriaca</i>	33.7
Shepherd's purse	<i>Capsella bursa-pastoris</i>	31.6
Flixweed	<i>Descurainia sophia</i>	29.5
Velvetleaf	<i>Abutilon theophrasti</i>	27.4
Giant ragweed	<i>Ambrosia trifida</i>	25.2
Waterpod	<i>Hydrolea quadrivalvis</i>	25.2
Wild lettuce	<i>Lactuca virosa</i>	25.2
Catnip	<i>Nepeta cataria</i>	23.1
Leafy spurge	<i>Euphorbia esula</i>	23.1
Common water hemp	<i>Amaranthus tuberculatus</i>	23.1
Common mallow	<i>Malva neglecta</i>	21.0
Marijuana	<i>Cannabis sativa</i>	21.0
Purslane speedwell	<i>Veronica peregrina</i>	21.0
Silvery cinquefoil	<i>Potentilla argentea</i>	18.9
Alsike clover	<i>Trifolium hybridum</i>	16.8
Russian thistle	<i>Salsola tragus</i>	16.8
Catchweed bedstraw	<i>Galium aparine</i>	16.8
Buffalobur	<i>Solanum rostratum</i>	14.7
Stinging nettle	<i>Urtica dioica</i>	14.7
Common burdock	<i>Arctium minus</i>	14.7
Common groundsel	<i>Senecio vulgaris</i>	12.6
Spiny thistle	<i>Sonchus asper</i>	12.6
Venice mallow	<i>Hibiscus trionum</i>	12.6
Wild rose	<i>Rosa sp.</i>	12.6
Black mustard	<i>Brassica nigra</i>	10.5
Motherwort	<i>Leonurus cardiaca</i>	10.5
Wild mustard	<i>Sinapis arvensis</i>	10.5
Redroot pigweed	<i>Amaranthus retroflexus</i>	8.4
Blue violet	<i>Viola sororia</i>	8.4
Indian mustard	<i>Brassica juncea</i>	8.4
Red clover	<i>Trifolium pratense</i>	8.4
Pennsylvania smartweed	<i>Polygonum pennsylvanicum</i>	8.4
Wormwood	<i>Artemisia absinthium</i>	8.4
Pineapple weed	<i>Matricaria discoidea</i>	6.3
Broadleaf plantain	<i>Plantago major</i>	6.3
Wild garlic	<i>Allium vineale</i>	6.3
Hedge bindweed	<i>Calystegia sepium</i>	4.2
Horsetail	<i>Equisetum arvense</i>	4.2
Woolyleaf bursage	<i>Ambrosia eriocentra</i>	4.2
Purple deadnettle	<i>Lamium purpureum</i>	2.1
Alfalfa	<i>Medicago sativa</i>	2.1
Small-flowered bittercress	<i>Cardamine parviflora</i>	2.1
Blackseed plantain	<i>Plantago rugelii</i>	2.1
Common chickweed	<i>Stellaria media</i>	2.1
Field horsetail	<i>Equisetum spp.</i>	2.1
Moth mullein	<i>Verbascum blattaria</i>	2.1
Musk mallow	<i>Malva moschata</i>	2.1
Purple poppy mallow	<i>Callirhoe involucrata</i>	2.1
Prostrate knotweed	<i>Polygonum aviculare</i>	2.1
Wild onion	<i>Allium ascalonicum</i>	2.1
Yellowspine thistle	<i>Cirsium ochrocentrum</i>	2.1

study reported HG type 0 to be the predominant HG type in South Dakota (Acharya et al. 2016); therefore, HG type may have had minimum impact on the probability to detect a weed as a host for SCN under field conditions in this study.

Table 2. Average number of soybean cyst nematodes obtained from the sampled counties of South Dakota.^a

County	No. of fields	Average no. eggs per 100 cm ³	Range
Bon Homme	3	2,375	1,800–3,300
Brookings	10	3,770	2,200–11,500
Clay	3	1,767	1,500–1,900
Deuel	1	1,600	–
Grant	1	700	–
Hamlin	2	1,500	1,400–1,600
Hanson	3	1,667	1,200–2,300
Hutchinson	3	1,733	900–2,700
Lincoln	4	4,050	2,900–7,000
McCook	1	2,600	–
Minnehaha	1	1,800	–
Roberts	2	2,000	1,500–2,500
Turner	10	1,390	1,200–100,000

^aExpressed as average number of eggs per 100 cm³ of soil sampled.

Table 3. Number of soybean cyst nematode (SCN) juveniles found in various weed species collected from 48 previously confirmed SCN fields in South Dakota.

Weed	No. of fields with the weed species	Average number of SCN juveniles across weed species	Range
Common cocklebur	7	2.1	1–2
Common mallow	1	2.0	–
Canada thistle	6	1.7	1–2
Field pennycress	24	4.9	1–19
Horseweed	1	2.0	–
Leafy spurge	6	1.8	1–3
Purple deadnettle	1	16.0	–
Small-flowered bittercress	1	2.0	–
Purple poppy mallow	1	1.0	–
Shepherd's purse	2	2.0	1–3
Venice mallow	1	15.0	–
White clover	18	4.9	1–20

Table 4. Total number of soybean cyst nematode females (cysts) formed and their respective female index for weed samples in a greenhouse confirmation experiment.^a

Weed species	Average number of cysts	Female index % ^a
Common cocklebur	0.38	1.10
Common mallow	0.69	2.04
Canada thistle	0.44	1.24
Field pennycress	10.2	26.9
Purple deadnettle	12.3	34.6
Shepherd's purse	0.63	1.89
White clover	1.86	1.86

^aFemale index was obtained by dividing the number of cysts in a weed species divided by the cysts in the susceptible check $\times 100$. Data were pooled across the two greenhouse runs.

Purple deadnettle and field pennycress had the highest FIs of 34.6% and 26.9%, respectively, among the weeds tested as hosts in the greenhouse. FIs were lower for common mallow (FI = 2.04), shepherd's purse (FI = 1.89), Canada thistle (FI = 1.24), white clover (FI = 1.86), and common cocklebur (FI = 1.10) (Table 4). Horseweed, Venice mallow, and leafy spurge did not support cyst development in the greenhouse, although roots from these species collected from the field were found with SCN juveniles.

This study identified and confirmed weed species that are hosts for SCN in South Dakota. Among the 63 commonly found weed species sampled and tested, 12 weed species were found with juveniles in the roots. Of these 12 weeds, 7 (field pennycress, purple deadnettle, common mallow, shepherd's purse, white clover, common cocklebur, and Canada thistle) supported SCN cyst development in the greenhouse. Except common mallow, all the other weed hosts determined from this study had been previously identified as SCN weed hosts in other states. The number of cysts that formed on these roots was 70% to 99% lower than a susceptible soybean variety. These data suggest that the majority of the weeds tested above are poor hosts, and only a small portion of juveniles can complete their life cycle on these weed species. The few weeds that supported completion of SCN life cycle, however, may serve as a bridge for SCN in fields when not planted to soybean.

Canada thistle, common cocklebur, shepherd's purse, white clover, and common mallow supported low SCN cyst development (FI < 5%) and therefore can be categorized as poor hosts for SCN. Our results are in agreement with a few previous reports but also differ from some of these reports. For instance, Poromarto et al. (2015) also found Canada thistle and common cocklebur to be a poor host for SCN; however, Wong and Tylka (1994) and Venkatesh et al. (2000) found these weeds not to be SCN hosts. Similarly, shepherd's purse was found to be a poor host of SCN in this study, as was also reported by Venkatesh et al. (2000) and Johnson et al. (2008). However, Poromarto et al. (2015) reported shepherd's purse as a non-host species. Additionally, white clover was found to be a poor host of SCN in our study, in agreement with findings by Donald et al. (2007) and Warner et al. (2017). However, no SCN cysts were found on this weed in the greenhouse study by Poromarto et al. (2015). The difference in classification of SCN weed hosts in different studies might be attributable to differences in SCN HG types as well as weed biotypes used in these studies.

The weed species that supported cyst development in this study can be categorized in the host range types as determined by Riggs (1987). Interestingly, Canada thistle, cocklebur, shepherd's purse, white clover, and common mallow did not support cyst development in all the replicates in the greenhouse, suggesting again that these weed species are poor SCN hosts (Poromarto et al. 2015). Weeds such as purple poppy mallow, horseweed, Venice mallow, and leafy spurge did not support cyst development under the greenhouse conditions. This result can be explained by the observation that certain weed species only allow penetration and juvenile development but do not allow completion of the cyst development as reported by Riggs (1987). Such weed species might play an important role as a trap crop, where juveniles can penetrate but cannot form cysts. Field pennycress and purple deadnettle supported development of several cysts; therefore, these two weeds can be categorized as good SCN hosts in South Dakota.

Weed species compete with soybean for water and nutrients and may allow continued development of SCN inoculum in the field by serving as alternative weed hosts (Bernards and Sandell 2011; Nice and Johnson 2005). Results from this study suggest that field pennycress and purple deadnettle are important SCN weed hosts from the SCN management point of view, as they can support significant SCN reproduction in the field and the greenhouse. However, the abundance of field pennycress in the soybean fields in South Dakota elevates its importance as a major alternative SCN weed host. Moreover, increasing interest of researchers in studying field pennycress as a potential cover crop or oilseed crop, and as integration to a corn-soybean rotation system further implicates

its importance as a SCN weed host (Bishop and Nelson 2019). These research findings suggest that weed species that are SCN hosts should be proactively controlled in fields that are positive for SCN to limit the spread and continued accumulation in the soil in the absence of soybean.

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