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Likelihood of Soybean Cyst Nematode (*Heterodera glycines*) Reproduction on Henbit (*Lamium amplexicaule*) Roots in Nebraska

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Soybean cyst nematode (SCN) is a major soybean yield–limiting disease in the United States. Henbit, a winter annual species common to no-till fields in the midwestern United States, is known to act as an alternative host for SCN. A simulation was performed to estimate how likely SCN was to reproduce on henbit roots during a 30-yr period in two important soybean production areas of Nebraska. Simulations were conducted using published information on henbit seedling emergence, SCN reproduction on henbit roots, and SCN response to soil temperature. Results indicate that SCN would be able to complete one generation on henbit roots under Nebraska conditions. The SCN reproductive cycle was not likely to be completed before the winter in south central Nebraska, but one SCN generation was predicted to be completed in the fall in 2 out of 30 simulation years (7% likelihood) in southeast Nebraska. Based on our predictions, to reduce the chances of SCN population build-up in the absence of its main host (soybean), weed management in fields infested with both henbit and SCN should be completed after crop harvest in the fall when most henbit seedlings have emerged and are growing but the SCN developing on henbit roots have not yet achieved full maturity in Nebraska.

Nomenclature: Henbit, *Lamium amplexicaule* L. LAMAM; soybean cyst nematode, *Heterodera glycines* Ichinohe.

Key words: SCN reproduction, SCN alternative host, winter annual weed, thermal time.

El nematodo cístico de la soja (SCN) es la enfermedad que más limita el rendimiento de la soja en los Estados Unidos. *Lamium amplexicaule* es una especie anual de invierno común en campos con labranza cero, y que se conoce que actúa como hospedero alternativo de SCN. Se realizó una simulación para estimar qué tan probable fue la reproducción de SCN en raíces de *L. amplexicaule* durante un período de 30 años en dos áreas importantes de soja en Nebraska. Las simulaciones se realizaron usando información publicada acerca de la emergencia de plántulas de *L. amplexicaule*, reproducción de SCN en raíces de *L. amplexicaule*, y la respuesta de SCN a la temperatura del suelo. Los resultados indican que SCN podría ser capaz de completar una generación en raíces de *L. amplexicaule* en las condiciones de Nebraska. No fue probable que el ciclo reproductivo de SCN se completara antes del invierno en el sur-central de Nebraska, pero se predijo que se completaría una generación de SCN en el otoño en 2 de los 30 años de simulación (7% de probabilidad) en el sureste de Nebraska. Con base en nuestras predicciones, para reducir las oportunidades de aumentos en las poblaciones de SCN en ausencia de su hospedero principal (soja) en Nebraska, el manejo de malezas en campos infestados con *L. amplexicaule* y SCN debe ser completado después de la cosecha del cultivo en el otoño, cuando las plántulas de *L. amplexicaule* han emergido y están creciendo, pero el SCN que está desarrollándose en raíces de *L. amplexicaule* no ha alcanzado la madurez.

Soybean cyst nematode (SCN) is considered the most yield-limiting disease of soybean in the United States (Wrather and Koenning 2006). SCN is an endoparasitic plant nematode that is currently found in most states where soybean is cultivated. In Nebraska, SCN presence has been confirmed in 52 of 93 counties (Giesler and Wilson 2011). SCN can damage host plants by removing essential nutrients from the root cells and disrupting the root vascular system, reducing water and nutrient uptake and transport from the roots to aboveground biomass (Asmus and Ferraz 2002; Hershman 1997). Additionally, SCN infection can indirectly damage soybean by reducing rhizobium nodulation and facilitating the occurrence of some diseases caused by other soilborne pathogens (e.g., sudden death syndrome, Rhizoctonia seeding blight, charcoal rot) (Hershman 1997; Wrather et al. 1984). Soybean

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Figure 1. Henbit plants flowering in a no-till field infested with soybean cyst nematode in southeast Nebraska before crop planting in the spring. (Color for this figure is available in the online version of this paper.)

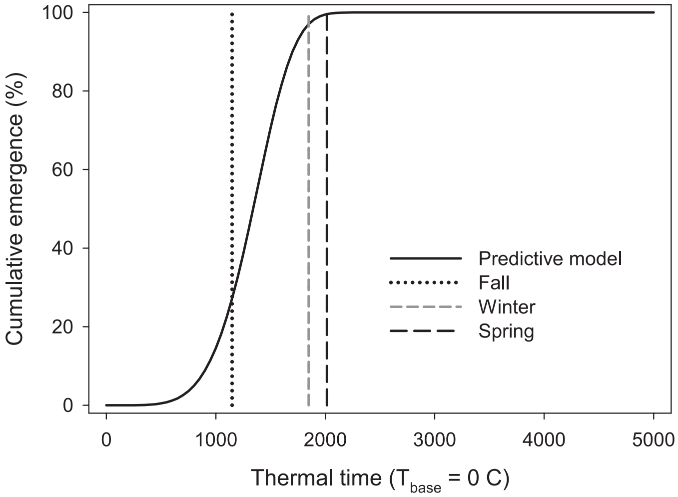

Figure 2. Predictive model of henbit emergence ($CE = 100\{1 - \exp[-\exp(-36.7810)(sGDD^{5.0569})]\}$, where CE is cumulative seedling emergence (%) and sGDD is soil growing degree days; adapted from Werle et al. (2014)). Accumulation of thermal time started on August 1. Fall, winter, and spring vertical lines represent the soil thermal time accumulated by the beginning of each season, respectively, averaged across the eight experimental year-sites where the emergence studies were conducted.

yield reductions of up to 30% have been caused by SCN without visually detectable aboveground symptoms (Noel 1992). The use of SCN-resistant varieties and rotation with nonhost crops (e.g., corn, *Zea mays* L.; sorghum, *Sorghum bicolor* L.; or wheat, *Triticum aestivum* L.) are the main strategies recommended for SCN management (Niblack 2005).

Winter annual weeds have become prolific in U.S. row crops because of the increased adoption of conservation tillage practices (Swagata et al. 2009), widespread adoption of glyphosate-resistant crops (Owen and Zelaya 2005), and the reduced use of residual herbicides (Shaner 2000). Winter annuals can result in delayed soil warming (Lee and Witt 2001), competition for nutrients and water during initial establishment of the main crop (Bernards and Sandell 2011), and difficult planting operations (Krausz et al. 2003). Moreover, several winter annual weeds, including henbit and purple deadnettle (*Lamium purpureum* L.), have been reported as alternative hosts of SCN (Creech et al. 2007a; Venkatesh et al. 2000; Werle et al. 2013). SCN reproduction on henbit and purple deadnettle roots in fields of the midwestern United States has been reported (Creech et al. 2005, 2007c). Henbit is one of the most prevalent winter annual weed species in no-till fields in Nebraska (Figure 1), with more than 95% of its seedlings expected to emerge in the fall (Figure 2; Werle et al. 2014). Therefore, SCN reproduction may occur and SCN populations increase between crop harvest and planting in fields where henbit is prevalent and not controlled in the fall.

Temperature is a major environmental factor influencing SCN development on susceptible hosts (Alston and Schmitt 1988). The basal temperature for SCN development has been estimated to be 5 C (Alston and Schmitt 1988). Low temperatures during the time that winter annual weeds are growing can be a limiting factor for SCN reproduction on the roots of these alternative hosts. The objective of this simulation work was to estimate the likelihood of SCN accomplishing at least one complete lifecycle on henbit roots based on heat unit accumulation under Nebraska field conditions.

Materials and Methods

Description of Simulation Sites. Lincoln Agronomy Farm, Lincoln, in southeast Nebraska (LAF: 40.8532N, 96.6168W; altitude 362 m) and South Central Agricultural Laboratory, Clay Center, in south-central Nebraska (SCAL: 40.5793N, 98.1385W; altitude 557 m) were chosen as our simulation sites because they represent two important soybean production areas of Nebraska where henbit and SCN are known to be present. The sites used for our simulations have been in a corn–soybean rotation for the past 10 yr. The soil at LAF is an Aksarben silty clay loam (clay, silt, sand, and organic matter content were 27, 54, 19, and 3%, respectively) and the soil at SCAL is a Hastings silt loam (clay, silt, sand, and organic matter content were 20, 57, 23, and 2.3%, respectively).

Predicting Henbit Emergence. Daily soil temperature at 2-cm depth at LAF and SCAL were estimated for a 30-yr period (1983–2013) using STM^2, a model for predicting soil microclimate conditions (Spokas and Forcella 2009). STM^2 requires daily maximum and minimum air temperature, daily precipitation, soil properties (sand, silt, clay, and organic matter content), latitude, longitude, and elevation of the simulation site for microclimate predictions. Daily maximum and minimum air temperature and precipitation during the 30-yr period were obtained from the nearest automated weather station (High Plain Regional Climate Center; www.hprcc.unl.edu), located within 1 km of the simulation sites, and soil properties described previously were assumed to be constant over the entire period. To evaluate the accuracy of STM^2 predictions, estimated daily soil temperature was regressed on measured soil temperature at 2-cm depth from August 2010 through July 2011 at LAF and SCAL (Werle et al. 2014). A linear regression was fit to the data using SigmaPlot 10.0 (Systat Software Inc., San Jose, CA) to estimate the correlation between estimated and measured soil temperature.

The estimated daily soil temperature at each year-site was then used to accumulate soil growing degree days (sGDD) to predict time to 50% henbit emergence (Werle et al. 2014) and to first and second SCN complete generations, respectively. The base temperature (T_{base}) used to accumulate heat units to predict henbit emergence and SCN development on henbit roots were 0 and 5 C, respectively (Alston and Schmitt 1988; Werle et al. 2014). sGDD accumulation was calculated as:

$$\text{sGDD} = \sum\nolimits_{i=1}^{n} (T_{\text{mean}} - T_{\text{base}}) \qquad [1]$$

where i is the starting date to accumulate thermal time, n is the number of days after i, T_{mean} is the mean daily soil temperature (C), and T_{base} is temperature below which the process of interest does not occur (C). When $T_{\text{mean}} > T_{\text{base}}$, $T_{\text{mean}} - T_{\text{base}}$ heat units were accumulated on a daily basis; when $T_{\text{mean}} < T_{\text{base}}$, no accumulation of heat units took place.

Prediction of time to 50% henbit emergence was based on data collected at eight year-sites across Nebraska (Werle et al. 2014),

$$\text{CE} = 100\{1 - \exp[-\exp(-36.7810) \times (\text{sGDD}^{5.0569})]\} \qquad [2]$$

where CE is cumulative seedling emergence (%). Accumulation of sGDD started on August 1 of each year. According to the predictive model, 50% henbit emergence took place at approximately 1,341 sGDD ($T_{\text{base}} = 0$ C; Figure 2).

Predicting SCN Reproduction on Henbit Roots. Results reported by Werle et al. (2013) were used to predict SCN development. Their preliminary studies showed that the first SCN cysts could be found on henbit and soybean roots within 21 d of inoculating them with SCN eggs when growing under controlled environment (soil temperature at 27 C). At 28 d after inoculation (DAI) with 1,000 SCN eggs, they found 73 cysts plant^{-1}, 288 cysts g root^{-1}, 208 eggs cyst^{-1}, and 15,234 eggs plant^{-1} in henbit roots. At 56 DAI, after the completion of a second SCN generation, 546 cysts plant^{-1}, 1,132 cysts g root^{-1}, 124 eggs cyst^{-1}, and 68,125 eggs plant^{-1} were detected in henbit roots (R. Werle, unpublished data). Increases of approximately 7.5-fold cysts plant^{-1}, 4.0-fold cysts (g root)$^{-1}$, and 4.5-fold eggs plant^{-1} were detected from 28 to 56 DAI. 617 and 1,242 sGDD ($T_{\text{base}} = 5$ C) were accumulated at 28 and 56 DAI, respectively. Similarly, Alston and Schmitt (1988) reported that, under field conditions, SCN required 534 sGDD ($T_{\text{base}} = 5$ C) to complete a generation on its primary host, soybean. We used 617 and 1,242 sGDD values as the reference thermal time required for SCN to complete first and second generations, respectively, on henbit roots.

Statistical Analysis. Estimated soil temperatures from the 30 yr of historical weather data were used to predict time (day of year) to 50% henbit emergence and SCN reproduction on henbit roots at each year-site. Accumulation of sGDD for the onset of SCN development on henbit roots at each year-site started when 50% henbit emergence was

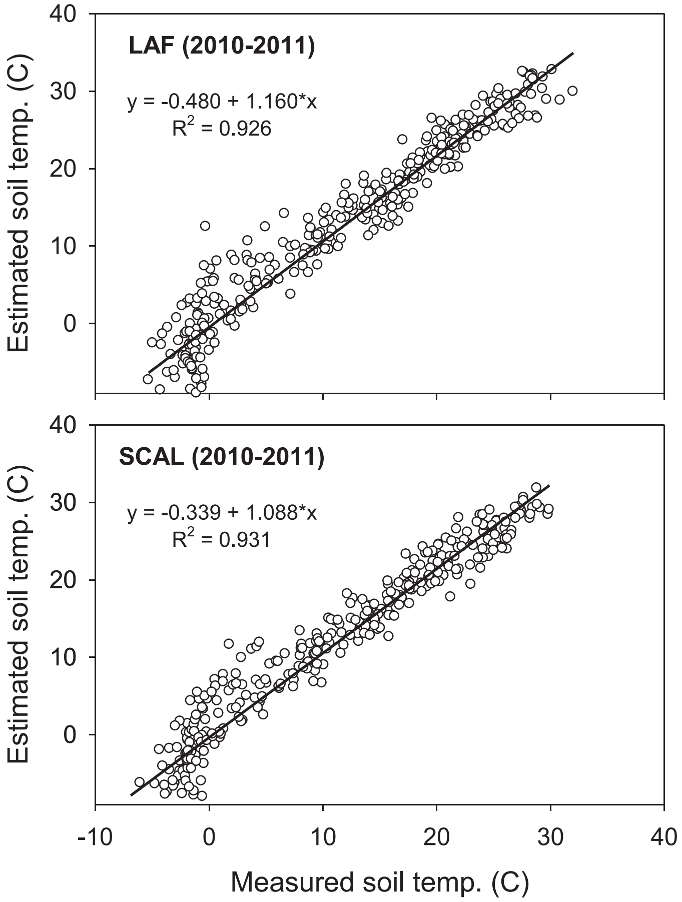

Figure 3. Relationship between estimated and measured soil temperature at 2-cm depth at Lincoln Agronomy Farm (LAF) and South Central Agricultural Laboratory (SCAL). Measured temperature was recorded from August 2010 through July 2011 at each site.

predicted. The time to 50% henbit emergence and SCN first and second complete cycle on henbit roots were subjected to ANOVA using PROC GLIMMIX in SAS 9.2 (SAS Institute, Cary, NC). Experimental sites were treated as fixed factors, and years were treated as replications (30 yr for each site). Means were separated when main effect was $<P = 0.05$.

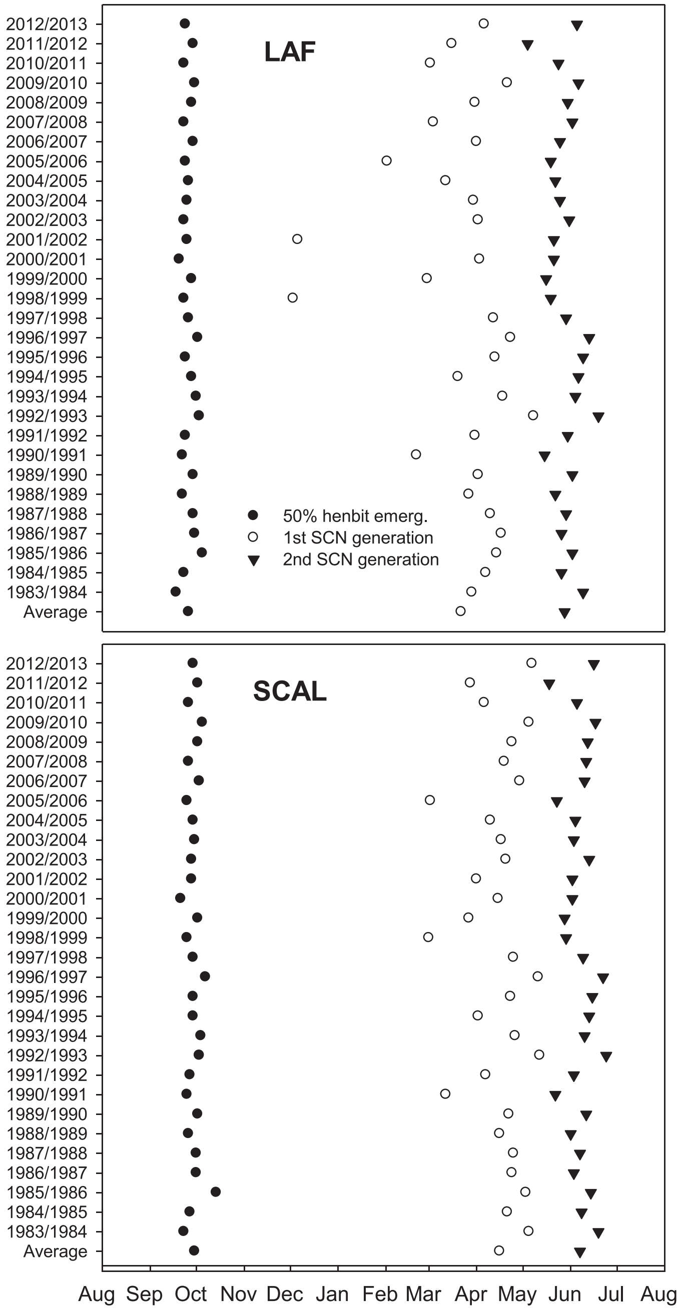

Figure 4. Predicted time to 50% henbit emergence and to complete a first and second SCN generation on henbit roots, respectively, for each year-site (Lincoln Agronomy Farm [LAF], South Central Agricultural Laboratory [SCAL]).

Results and Discussion

A high correlation ($R^2 > 0.92$) between estimated and measured soil temperature was detected for both sites, indicating high accuracy of STM^2 soil temperature estimations (Figure 3). Spokas and Forcella (2009) also reported high STM^2 accuracy when simulating soil temperature at multiple locations. Thus, STM^2 can be a powerful tool to simulate soil temperature when these data are not available. Time to 50% henbit emergence was predicted to occur on September 25 ± 1 d and September 29 ± 1 d (average ± SE) at LAF and SCAL, respectively (Figure 4). The first SCN generation was predicted to be completed on March 21 ± 7 d and April 15 ± 3 d at LAF and SCAL,

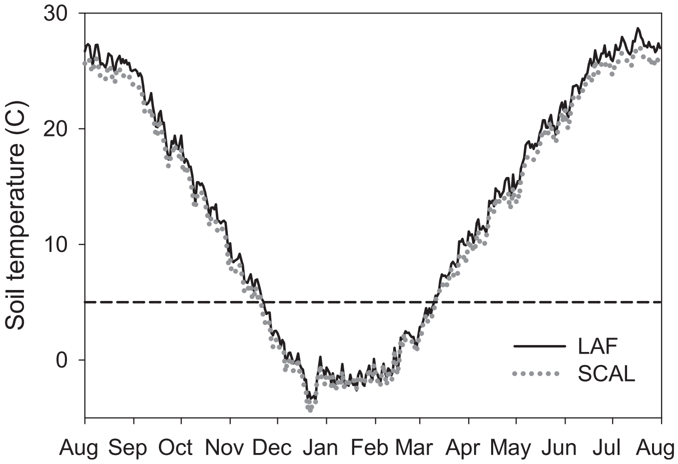

Figure 5. Thirty-year (1983–2013) estimated average soil temperature at 2-cm depth at Lincoln Agronomy Farm (LAF) and South Central Agricultural Laboratory (SCAL). Dashed line represents the base temperature for soybean cyst nematode development (5 C).

respectively (assuming that winter will have no effect on completion of an SCN generation). Completion of a second SCN generation was estimated on May 27 ± 2 d and June 6 ± 2 d, at LAF and SCAL, respectively, time when henbit plants are starting to senesce in Nebraska (R. Werle, field observation). Henbit emergence and first and second SCN complete generation were slightly delayed at SCAL when compared with LAF ($P = 0.003$, 0.001, and < 0.001, respectively) because of the overall lower temperatures during the year at SCAL compared with LAF (Figure 5). The Lincoln Agronomy Farm is located within the Lincoln city limits and exhibits characteristics of an urban heat island, where temperatures can be slightly greater (1 to 2 C) than surrounding agricultural areas. Creech et al. (2007b) reported that SCN juveniles survived for at least 20 d at 0 C in purple deadnettle roots and continued their development when temperatures became favorable again. This indicates that if SCN cannot complete its lifecycle in the fall, it can go dormant during winter and resume development in the spring.

A first complete SCN generation in the fall was only predicted during 2 yr at LAF (1998 and 2001), a 7% likelihood. At SCAL, SCN was not predicted to complete a reproductive cycle during the fall of any year (0% likelihood; Figure 4). This indicates that a complete SCN generation on henbit roots in the fall is not very likely under Nebraska conditions. The amount of sGDD used for our simulations assumed a complete SCN life cycle (formation of fully developed SCN cysts). However, immature SCN cysts could be observed on henbit roots before this period. Conversely, Creech et al. (2007c) found SCN cysts to be the prevalent SCN developmental stage in henbit and purple deadnettle roots during their fall sampling in field surveys conducted in Illinois, Indiana, and Ohio, whereas juvenile stages were prevalent in the spring. Therefore, SCN was able to accomplish at least one complete reproductive cycle in the fall and a second generation was already developing on the roots of these alternative hosts in the spring at those locations. Harrison et al. (2008) also reported that SCN completed one generation in purple deadnettle roots before onset of winter in Ohio. Thirty year average monthly temperatures during October and November were substantially greater in Illinois and Indiana than in Nebraska, which may favor SCN reproduction in the fall in those eastern states (Table 1).

According to our simulations, a second SCN generation developing on henbit roots would not be accomplished before late May (Figure 4). The corn planting season begins, is most active, and ends on April 19, April 27 to May 15, and May 21, respectively, in Nebraska. For soybean, the average

Table 1. Thirty-year average monthly temperatures (C) from 1981 to 2010 at some of the sites surveyed by Creech et al. (2007c) in Illinois (IL) and Indiana (IN) and sites in Nebraska (NE) used in this study.[a,b]

		September			October			November		
Site	State	Min	Avg	Max	Min	Avg	Max	Min	Avg	Max
Carmi	IL	13.2	19.9	26.7	6.7	13.7	20.8	1.6	7.4	13.3
Vincennes	IN	13.8	20.5	27.1	7.9	14.4	20.8	2.3	7.7	13.1
Clay Center	NE	10.9	18.2	25.4	4.1	11.2	18.4	−3.0	3.6	10.1
Lincoln	NE	11.2	18.4	25.7	4.1	11.4	18.7	−2.9	3.6	10.0

[a] Data obtained from NOAA (National Climatic Data Center; http://www.ncdc.noaa.gov/cdo-web/datatools/normals).

[b] Min, minimum; Max, maximum, Avg, average.

dates are May 5, May 11 to May 31, and June 8, respectively (USDA 2010). Therefore, in ordinary years, SCN would only be able to complete one generation on henbit roots under Nebraska conditions if growers controlled winter annual weeds before corn planting. In soybean, late planting along with late winter annual weed management is the scenario that would most likely allow for a second complete SCN life cycle on henbit roots. Thus, if henbit is managed before crop planting in the spring, a second SCN generation could be reduced or even prevented. SCN development may also be influenced by soil texture, moisture, and pH (Alston and Schmitt 1988). Therefore, it is important to acknowledge that our results should be used as general guide rather than absolute predictor of SCN development on henbit hosts.

Nelson et al. (2006) reported that SCN population density increased between fall and spring when winter annual weed hosts of SCN were not controlled. However, when herbicides were fall-applied, SCN population remained constant between fall and spring. On the other hand, Creech et al. (2008) found that in fields with low winter annual weed densities, weed control had no effect on SCN populations because so few weeds were present to facilitate SCN population growth. The continuation of this study showed that even under high winter annual weed infestations, weed management had no effect on SCN population density, and the authors concluded that winter annual weed control would have little effect as an SCN management strategy (Mock et al. 2012). One possible reason for the Mock et al. (2012) findings is the relatively low SCN egg density in the research sites where their studies were conducted (averages ranging from 22 to 170 eggs $(100\ \mathrm{cm})^{-3}$ of soil). Conversely, Harrison et al. (2008) found that when purple deadnettle was removed within 4 wk after emergence (WAE; 389 sGDD; $T_{\mathrm{base}} = 5$ C), SCN egg population density did not increase. However, an increase in SCN egg population density was detected when purple deadnettle was removed after 4 WAE ($>$ 389 sGDD). SCN egg density ranged from 20 to 7,800 eggs $(100\ \mathrm{cm})^{-3}$ of soil in their study. This corroborates the findings of Werle et al. (2013), who found herbicide application at approximately 308 sGDD ($T_{\mathrm{base}} = 5$ C) reduced SCN reproductive potential on henbit roots in controlled environments.

Crop rotation and use of resistant soybean varieties are the current practices recommended for SCN management. Perhaps winter annual weed control in the fall should be added to this list (Nelson et al. 2006; Venkatesh et al. 2000). According to our simulations, SCN is not very likely to accomplish one generation before winter, and a second complete generation would only be expected if henbit was not controlled until late May or early June under a typical season in Nebraska. Therefore, fall management of established henbit plants in agricultural fields infested with SCN could reduce the likelihood of increasing SCN population density on henbit roots because SCN is not likely to have achieved the reproductive stage at this time. Werle et al. (2013) showed that if henbit is managed early enough, SCN reproduction potential will be reduced or even prevented completely. Moreover, a fall herbicide application has been shown to provide satisfactory winter annual weed control (Hasty et al. 2004) and is especially beneficial before a wet spring (Krausz et al. 2003). Furthermore, winter annual weeds are more susceptible to herbicide treatments in the fall when they are small. During spring, herbicide application might not result in the desired control if these weeds are at an advanced growth stage (Johnson et al. 2008), and SCN reproduction may no longer be prevented or reduced (Werle et al. 2013).

SCN reproduction on henbit roots can be expected if (1) environmental conditions are adequate for both organisms to grow, (2) enough host plants and pathogen inoculum (SCN eggs) are present to support SCN population growth, and (3) both SCN and alternative host distribution within a field overlap, since nematode movement is limited. Thus, future research to identify the critical population density of both alternative winter annual weed hosts and SCN inoculum that results in nematode population build-up under field conditions is needed. Moreover, knowledge of SCN overwintering survival on winter annual weed hosts under field conditions is still needed.

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