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Characterization of *Heterodera sojae* Virulence Phenotypes in Korea

Heonil Kang[1], Hyoungrai Ko[2], Byeongyong Park[2], and Insoo Choi [3,4]*

[1]*Forest Entomology and Pathology Division, National Institute of Forest Science, Seoul 02455, Korea*
[2]*Division of Crop Protection, National Institute of Agricultural Science, Rural Development Administration, Wanju 55365, Korea*
[3]*Nematode Research Center, Life and Industry Convergence Research Institute, Pusan National University, Miryang 50463, Korea*
[4]*Department of Plant Bioscience, College of Natural Resource and Life Sciences, Pusan National University, Miryang 50463, Korea*

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The white soybean cyst nematode *Heterodera sojae*, isolated from the roots of soybean in Korea, is widespread in most provinces of the country and has the potential to be as harmful to soybean as *H. glycines*. Determining the virulence phenotypes of *H. sojae* is essential to devising management strategies that use resistant cultivars. Consequently, virulence phenotypes of 15 *H. sojae* populations from Korea were determined on seven soybean lines and one susceptible check variety. Two different HS types were found to be present in Korea; the more common HS type 2.5.7, comprising 73.3% of the *H. sojae* populations and the less common HS type 0, constituting only 26.7% of the tested populations. Considering the high frequency of *H. sojae* adaptation to soybean indicator lines, the PI 88788 group may not be a possible source of resistance while PI 548402, PI 90763, PI 437654, and PI 89772 can be used as resistance sources for soybean breeding programs aimed at developing *H. sojae*-resistant soybean cultivars in Korea.

*Corresponding author.
Phone) +82-55-350-5504, FAX) +82-55-350-5509
E-mail) ichoi@pusan.ac.kr
ORCID
Insoo Choi
https://orcid.org/0000-0002-5745-579X

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Soybean [*Glycine max* (L.) Merr.] is a globally important food crop that is recognized to be a key source of nutrition worldwide. Soybean has a long history of cultivation in Korea and is one of the five major crops grown. In fact, soybean seeds dating from approximately 2,720-2,380 BCE were discovered at Neolithic dwelling sites in several places along the Daundong and Nam River basin, Korea (Lee et al., 2011).

Over 4,100 species of plant-parasitic nematodes have been described, and several of these are known to cause serious yield losses in crops (Decraemer and Hunt, 2006; Jones et al., 2013). Among the plant-parasitic nematode species, the soybean cyst nematode (*Heterodera glycines*) is the most limiting biotic factor in soybean production worldwide. Soybean yield losses due to *H. glycines* are commonly 10-20%, while reductions in production of up to 30% can occur even without showing any visible symptoms. Nematodes have been estimated to cause two times the yield losses compared to any other soybean diseases in the United States and Ontario, Canada (Allen et al., 2017; Noel, 1992; Wang et al., 2003).

Heterodera glycines was identified in Japan in 1915, Korea in 1936, and Manchuria in 1938 (Riggs, 1977; Yokoo, 1936). The parasite has since become damaging in soybean fields in Korea. *H. glycines* has the particular ability to survive for prolonged periods of up to 20 years in soil without its host. Eggs are protected from heat, drying, chemicals, and other adverse environmental conditions by the protective cysts that are formed by eventual hardening and tanning of the cuticle of females (Epps, 1958; Grainger, 1964). The use of resistant varieties and non-host crops in rotation has proven to be a more effective and sustainable method of managing *H. glycines* than other control practices (Acharya et al., 2016; Auwal et al., 2014).

At first, the virulence phenotypes in *H. glycines* populations were identified by using four soybean varieties and a susceptible standard (Golden et al., 1970; Riggs and Schmitt, 1988). About 15 years after the adoption of this race test, a HG type test using seven plant introductions (PIs) was developed and revised (Niblack et al., 2002; Tylka, 2016).

The white soybean cyst nematode, *H. sojae*, was first described from the roots of soybean plants in Korea, almost a century after the first description of *H. glycines* (Kang et al., 2016). Outside Korea, the species has been recorded in China and Japan (Sakai and Kushida, 2019; Zhen et al., 2018). In Korea, more than 30% of cultivated soybean fields are infected with the two cyst nematodes. *H. sojae* is widespread in most provinces and has the potential to be as harmful to soybean as *H. glycines* (Kang et al., 2021).

Nematode virulence is defined as the ability of the nematode parasite to reproduce on a host plant that contains specific genes, otherwise conferring resistance (Blok et al., 2018; Turner et al., 1983; Vanderplank, 1978). Phenotypic diversity of cyst nematode species is typical, so it is prudent to test a number of populations from the field against potential sources of resistance for their virulence before selecting material for studies on breeding resistant varieties (Blok et al., 2018). Understanding the distribution of virulence phenotypes can therefore provide valuable information about the sustainable and effective use of resistant soybean cultivars and the knowledge needed to breed non-susceptible crops. As there is no report for the virulence phenotypes of *H. sojae*, the objective of this study was to determine the HS types in populations of *H. sojae* sampled in Korea based on the re-known HG type test.

Materials and Methods

Soil sample collection. To study the occurrence of cyst nematode species on soybean crops in Korea, 15 populations of *H. sojae* were collected from six provinces (Kang et al., 2021). *H. sojae* was identified using its morphology and genetic markers (Kang et al., 2016). The cyst nematode populations from the field were multiplied and maintained on soybean cy. “Lee 74” in d-20 cm pots.

Inoculum preparation. After 2 months of population increase, the soil and roots were poured into a 10 l plastic bucket with 5 l of water. Females and cysts were dislodged by rubbing the roots hard. Larger pieces of debris were eliminated by decanting and sieving the soil and roots through two nested sieves with pore sizes of 850 and 250 μm. Females and cysts were collected in the 250 μm sieve, and placed in a 50-ml glass homogenizer. The samples were ground to release the eggs and second-stage juveniles (J2s) from the cysts and females. The released eggs and J2s were washed through two nested sieves with pore sizes of 100 and 25 μm to eliminate coarse debris and unbroken females and cysts. The collected eggs and J2s were placed in a beaker, and the total numbers were approximated by counting them under a microscope.

Virulence analysis. Virulence was analyzed according to the HS type test procedures that involved seven indicator lines, PI548402 (“Peking”), PI 88788, PI 90763, PI 437654, PI 209332, PI 89772, and PI 548316 (“Cloud”), and a susceptible check (“Lee 74”) (Niblack et al., 2002). The soybean PIs and susceptible check variety used in this HS type study were provided by the University of Arkansas, USA. Seeds were germinated in vermiculite and transplanted at the cotyledon stage into d-10 cm clay pots containing fumigant-sterilized soil. As an inoculum, approximately 4,000 eggs and J2s were added to each pot. The pots were placed in a greenhouse and maintained at 25 ± 5°C for 5 weeks. Each treatment was replicated three times. After about 60 days of cultivation under greenhouse conditions, the soil and roots from the pots were placed in about 10 l of water, washed well, and stirred vigorously. To release cysts from roots, the water was then passed quickly through 850-μm and 250-μm pore-size sieves. The debris from the 850-μm sieve was discarded, and the females (cysts) from the 250-μm sieve were placed in a square “cyst counting dish” (100 mm × 15 mm, Falcon grid dish). The number of females was counted under a stereo microscope. The number of released females, from the roots of each of the PIs and the susceptible check, was used to calculate the female index (FI) as follows: FI = (average number of females found on indicator line/average number of females found on susceptible line) × 100. The HS type test was based on an average population phenotype as defined by its ability (FI ≥ 10 = “+”) or lack thereof (FI < 10 = “–”) to develop on a set of seven PIs and compared with the susceptible check variety “Lee 74.” The population was named according to the number associated with the soybean PIs on which it was virulent (FI ≥ 10) (Niblack et al., 2002; Riggs and Schmitt, 1988).

Data analysis. Descriptive statistics for the FI data were obtained using SAS ver. 9.4 (SAS Institute Inc., Cary, NC, USA). Pearson's product moment correlation was used to determine the association between the FI values for the soybean indicator lines. An average number of females from three replications was used to calculate the FI for each soybean line.

Results

The number of females reproduced on the standard variety "Lee 74" in this HS type testing study varied among the populations. The numbers of females were in the range 66-823 and averaged 243 females per pot. The HS type and number of females recovered on unrelated, because HS type 0 from the Sancheon and Gyeongsan populations produced 66 and 238 females per pot, respectively, whereas HS type 2.5.7 from the Damyang and Changyeong populations produced 79 and 823 females per pot, respectively (Table 1). The reasons for this variation were unclear.

Fifteen populations of *H. sojae* collected from different provinces in Korea were used for HS type testing. None of the *H. sojae* populations reared on PI 548402 (HS type indicator line #1) showed FI value of above 10%, the highest FI on this indicator line was 0.8%. PI 88788 (#2) had higher FI value of the *H. sojae* populations, with FI values of mostly above 10%. The highest FI among *H. sojae* populations reared on PI 88788 was 81.6%, and this sample came from Goheung. Ten of the *H. sojae* populations reared on PI 88788 were between 16.0% and 57.1%, while four populations showed FI values of less than 10%. All populations tested on PI 90763 (#3) showed FI value of less than 10%, the highest FI value on this indicator line was 3.8%. On PI 437654 (#4), none of the populations had an FI ≥ 10%. The highest FI on this indicator line was 2.5%. Eleven of the *H. sojae* populations reared on PI 209332 (#5) showed FI values of above 10%. The highest FI on this indicator line was 85.7% (from Damyang), and the rest (10 of the 11) of the *H. sojae* populations had FI values of between 13.5% and 73.3%. All the populations that were experimented on PI 89772 (#6) showed FI values of less than 10%. Eleven of *H. sojae* populations reared on PI 548316 (#7) showed FI values of above 10%, with FI values ranging between 32.1% and 97.9% (Table 1).

From these tests, we found that *H. sojae* has two HS types, 0 and 2.5.7. HS type 2.5.7 was the more common virulence phenotype, comprising 73.3% (11 of 15) of the *H. sojae* populations. HS type 0 was less common, making up 26.7% (4 of 15) of the populations (Table 2). Most of the *H. sojae* populations tested were able to parasitize PI 88788, PI 209332, and PI 548316, and none of the populations tested developed above FI value of 10% on PI 538402,

Table 1. HS types in *Heterodera sojae* populations in Korea

Source (city)	No. of females on Lee74	Indicator number and FI (%)[a]							HS type
		1	2	3	4	5	6	7	
		PI 548402	PI 88788	PI 90763	PI 437654	PI 209332	PI 89772	PI 548316	
Goheung	125	0.8	81.6	0.0	0.0	73.3	0.0	97.9	2.5.7
Damyang	79	0.0	31.7	3.8	2.5	85.7	1.3	78.1	2.5.7
Jangseong	198	0.0	53.4	0.0	0.0	37.0	0.3	39.4	2.5.7
Jinju	564	0.4	17.6	0.1	0.4	28.9	1.8	44.2	2.5.7
Gyeongsan	238	0.0	9.4	0.0	0.0	6.5	0.0	9.5	0
Changnyeong	823	0.4	21.6	0.1	0.0	18.8	0.2	68.4	2.5.7
Hongcheon	213	0.5	1.4	0.5	0.0	1.9	0.0	0.5	0
Hoengseong	186	0.5	1.8	1.8	1.6	1.6	1.1	2.5	0
Bonghwa	99	0.0	36.4	0.7	0.4	37.0	0.0	65.3	2.5.7
Goseong	355	0.3	24.3	0.2	0.1	17.2	0.0	54.7	2.5.7
Sancheong	66	0.5	2.5	0.5	0.5	1.0	0.0	2.0	0
Gyeongju	361	0.1	16.0	0.1	0.1	13.5	0.1	65.4	2.5.7
Cheongju	156	0.0	20.5	0.2	0.2	21.2	0.4	32.1	2.5.7
Jeongeup	104	0.3	32.7	0.3	0.3	30.8	1.0	50.0	2.5.7
Haenam	83	0.0	57.1	0.0	1.2	31.2	0.0	77.7	2.5.7

PI, plant introduction.
[a]FI = female index [(mean number of females on indicator line/mean number of females on Lee74) × 100].

Table 2. Frequencies of HS types of *Heterodera sojae* in soil samples collected in Korea

HS type	No. of populations[a]	Frequency (%)
0	4	26.7
2.5.7	11	73.3
Total	15	100.0

[a]Number of *Heterodera sojae* populations.

PI 90763, PI 437654, or PI 89772. The nematode populations grown on PI 548402, the major resistance source for breeding soybean varieties in the region, showed the lowest average FI value (0.3%). Similarly, PI 548402, PI 89772 (FI = 0.4%), PI 437654 (FI = 0.5%), and PI 90763 (FI = 0.6%) showed high levels of resistance. The *H. sojae* populations in Korea could grow and reproduce on PI 548316 (45.9%), on PI88788 (27.2%), and on PI 209332 (27.0%). PI 548316 was the least resistant line to the Korea populations of *H. sojae*. This line was infected by 45.9% of the tested *H. sojae* populations.

Pearson correlations were identified between the FIs of some of the soybean indicator lines used in the HS type experiment (Table 3). A positive correlation ($P < 0.05$) was shown between three lines, PI 88788, PI 209332, and PI 548316, which had relatively high FI values. PI 90763 and PI 89772 had the highest correlation coefficient (0.85).

Discussion

In 2016, a new cyst nematode that parasitizes soybean was described as *H. sojae* in Korea. The cuticles of *H. sojae* cysts are white to creamy colored when young and become brown-black and shiny over time. Conversely, the cuticles of *H. glycines* cysts are yellow when young and become brown but without a shiny appearance (Kang et al., 2016). The cyst wall thickness in *H. sojae* is significantly greater than that of *H. glycines*, therefore, the eggs of *H. sojae* are more protected from external harmful materials and harsh environments than those of *H. glycines* (Han et al., 2020). In our previous study, carried out during 2017-2018, *H. sojae* was detected in 116 of 343 soybean parasitic cyst nematode samples. *H. sojae* has since been detected in most of the soybean-growing regions of Korea, with an average population density of 71 cysts and 110 J2s per 300 cm^3 of soil (Kang et al., 2021). The use of resistant varieties has been an effective method of managing soybean parasitic cyst nematodes. For the effective development and use of the resistant varieties, however, knowledge about the virulence phenotypes and the frequencies of *H. sojae* populations is necessary.

The results of this study indicated that the *H. sojae* populations in the collected soil samples were of HS types 0 and 2.5.7. HS type 2.5.7 had an FI ≥ 10% on indicator lines 2, 5, and 7. An HS of type 0 meant that the populations were not virulent to any of the resistance sources. HS type 2.5.7 was the most prevalent among the *H. sojae* populations, suggesting that most of the *H. sojae* populations in the collected samples were virulent on PI 88788, PI 209332, and PI 548316. In 2013, six different HG types in 13 *H. glycines* populations were found in Korea. HG type 2.5 was the most frequent (30.8%), followed by HG type 2.5.7 (23.0%) (Kim et al., 2013). The HS type diversity in the *H. sojae* populations is a little lower than that in the *H. glycines* populations in Korea. In United States, eight different HG types in *H. glycines* populations have been found in South Dakota and Missouri, and nine different HG types of *H. glycines* populations have been identified in Minnesota (Acharya et al., 2016; Mitchum et al., 2007; Zheng et al., 2006). The results of the current study may be in part due to no resistant cultivars breeding program in Korea. Korean farmers are planting cultivars that are susceptible to *H. sojae* and *H. glycines*; hence, there is likely a lower genetic

Table 3. Correlation coefficients among soybean lines with resistance to *Heterodera sojae* based on the female index of Korea populations[a]

Indicator line	PI 548402	PI 88788	PI 90763	PI437654	PI 209332	PI 89772
PI 88788	−0.007 ns					
PI 90763	−0.273 ns	−0.057 ns				
PI 437654	−0.107 ns	−0.036 ns	0.378 ns			
PI 209332	−0.034 ns	0.729 **	0.146 ns	0.412 ns		
PI 89772	−0.207 ns	−0.050 ns	0.848 ***	0.041 ns	−0.050 ns	
PI 548316	−0.108 ns	0.779 ***	0.039 ns	0.103 ns	0.752 ***	0.012 ns

PI, plant introduction.
[a]Female index = [(mean number of females on indicator line/mean number of females on Lee74) × 100]. *, **, *** represent $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. ns, not significant at $P \geq 0.05$.

diversity of *H. glycines* and *H. sojae* as the nematodes have not yet adapted to the resistant cultivars (Kim et al., 1997).

Different races of *H. glycines* were found after cultivation of resistant varieties over several years in the United States. In Korea, selection and cultivation of resistant varieties has not taken place, but there are already six HG types (four races) of *H. glycines* and two HS types of *H. sojae* in soybean fields. This phenomenon can be interpreted by assuming that there are varieties that are resistant to soybean cyst nematodes among Korean wild or native soybean varieties. Soybean originated such a long time ago (2,720-2,380 BCE) in Korea and therefore, could have abundant genetic variation. It can be assumed that natural selection of resistant or tolerant varieties has occurred and that farmers have selected resistant varieties over thousands of years. For example, a Korean native soybean variety PI97100 is known to be the most tolerant variety grown in the United States (Boerma and Hussey, 1984).

Our results showed a significant correlation in FI values between the HS type indicator lines PI 90763 and PI 89772. Also, a significant correlation was observed between the HS type indicator lines PI 88788, PI 209332, and PI 548316. PI 548402, PI 90763, PI 437654, and PI 89772 are good sources of resistance for developing *H. sojae*-resistant soybean cultivars in Korea. Although *H. glycines* populations were found to reproduce on PI 548402 (7.7%), no populations could reproduce on PI 90763, PI 89772, or PI 437654 in Korea (Kim et al., 2013).

Although the breeding lines PI88788 and PI548402 are commonly used as sources of resistance, the indicator line PI 437654 exhibits the best resistance to all the populations of soybean parasitic cyst nematodes in Korea. In the United States, PI 437654, which shows high-level resistance to most *H. glycines* populations, was used to develop the resistant cultivar “Hartwig” (Anand, 1992). HS type indicator lines PI 90763 and PI 89772 are considered to be part of the PI 548402 group, and their resistance induces an early plant tissue response resulting in necrosis. Indicator lines PI 88788, PI 209332, and PI 548316 are considered to be part of the PI 88788 group (Colgrove and Niblack, 2008). PI 88788-type resistance against *H. glycines* requires high copy numbers of a *rhg1* resistance allele (*rhg1-b*) and PI 548316-type resistance requires low copy numbers of both a different *rhg1* resistance allele (*rhg1-a*) and a resistance allele at another locus, *Rhg4*. Resistance associated with *rhg1* primarily involves the impairment of vesicle trafficking through disruption of soluble NSF-attachment protein receptor complexes. In contrast, resistance via *Rhg4* is accompanied by the disturbance of folate homeostasis at *H. glycines* feeding sites due to changes in the enzymatic activity of serine hydroxymethyltransferase (Liu et al., 2017; Shaibu et al., 2020). Considering the frequency with which *H. sojae* has adapted on soybean indicator lines, the PI 88788 group may not be preferred for breeding resistance to soybean parasitic cyst nematode species. Information on novel genes and mechanisms for *H. glycines* resistance is limited, but in order to develop resistant varieties against Korean populations of soybean parasitic cyst nematodes, a combination of several resistance alleles such as that found in PI 548316-type resistance may be required.

In conclusion, soybean breeders should focus on incorporating resistance from PI 437654, PI 90763, and PI 89772 into cultivars that are adapted to growing conditions in Korea. To better manage soybean parasitic cyst nematodes, nematologists and agronomists must establish a new classification scheme for the determination of virulence phenotypes in *H. sojae*.

Conflicts of Interest

No potential conflict of interest relevant to this article was reported.

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References

Acharya, K., Tande, C. and Byamukama, E. 2016. Determination of *Heterodera glycines* virulence phenotypes occurring in South Dakota. *Plant Dis*. 100:2281-2286.

Allen, T. W., Bradley, C. A., Sisson, A. J., Byamukama, E., Chilvers, M. I., Coker, C. M., Collins, A. A., Damicone, J. P., Dorrance, A. E., Dufault, N. S., Esker, P. D., Faske, T. R., Giesler, L. J., Grybauskas, A. P., Hershman, D. E., Hollier, C. A., Isakeit, T., Jardine, D. J., Kelly, H. M., Kemerait, R. C., Kleczewski, N. M., Koenning, S. R., Kurle, J. E., Malvick, D. K., Markell, S. G., Mehl, H. L., Mueller, D. S., Mueller, J. D., Mulrooney, R. P., Nelson, B. D., Newman, M. A., Osborne, L., Overstreet, C., Padgett, G. B., Phipps, P. M., Price, P. P., Sikora, E. J., Smith, D. L., Spurlock, T. N., Tande, C. A., Tenuta, A. U., Wise, K. A. and Wrather, J. A. 2017. Soybean yield loss estimates due to diseases in the United States and Ontario, Canada, from 2010 to 2014. *Plant Health Prog.* 18:19-27.

Anand, S. C. 1992. Registration of ‘Hartwig’ soybean. *Crop Sci*. 32:1069-1070.

Auwal, H. M., Wang, H., Li, L., Kakar, K.-U. and Zheng, J. 2014. Utilization of plant materials for control of soybean cyst nematode. *Acta Agric. Scand. B Soil Plant Sci.* 64:392-397.

Blok, V. C., Tylka, G. L., Smiley, R. W., de Jong, W. S. and Daub, M. 2018. Resistance breeding. In: *Cyst nematode*, eds. by R. N. Perry, M. Moens and J. T. Jones, pp. 174-214. Centre for Agriculture and Bioscience International, Wallingford, UK.

Boerma, H. R. and Hussey, R. S. 1984. Tolerance to *Heterodera glycines* in soybean. *J. Nematol*. 16:289-296.

Colgrove, A. L. and Niblack, T. L. 2008. Correlation of female indices from virulence assays on inbred lines and field populations of *Heterodera glycines*. *J. Nematol*. 40:39-45.

Decraemer, W. and Hunt, D. J. 2006. Structure and classification. In: *Plant nematology*, eds. by R. N. Perry and M. Moens, pp. 3-32. Centre for Agriculture and Bioscience International, Wallingford, UK.

Epps, J. M. 1958. Viability of air-dried *Heterodera glycines* cysts. *Plant Dis. Rep*. 42:594-595.

Golden, A. M., Epps, J. M., Riggs, R. D., Duclos, L. A., Fox, J. A. and Bernard, R. L. 1970. Terminology and identity of infraspecific forms of the soybean cyst nematode (*Heterodera glycines*). *Plant Dis. Rep*. 54:544-546.

Grainger, J. 1964. Factors affecting the control of eelworm diseases. *Nematologica* 10:5-20.

Han, G. R., Kang, H., Choi, I. S., Kim, D, Yun, H. Y. and Kim, Y. H. 2020. Differential morphological, structural and biological characteristics of cysts in *Heterodera* species in Korea. *Plant Pathol. J*. 36:628-636.

Jones, J. T., Haegeman, A., Danchin, E. G. J., Gaur, H. S., Helder, J., Jones, M. G. K., Kikuchi, T., Manzanilla-López, R., Palomares-Rius, J. E., Wesemael, W. M. L. and Perry, R. N. 2013. Top 10 plant-parasitic nematodes in molecular plant pathology. *Mol. Plant Pathol*. 14:946-961.

Kang, H., Eun, G., Ha, J., Kim, Y., Park, N., Kim, D. and Choi, I. 2016. New cyst nematode, *Heterodera sojae* n. sp. (Nematoda: Heteroderidae) from soybean in Korea. *J. Nematol*. 48:280-289.

Kang, H., Ko, H., Kim, D. and Choi, I. 2021. Occurrence of the white soybean cyst nematode, *Heterodera sojae*, and the soybean cyst nematode, *H. glycines*, in Korea. *Plant Dis*. 105:31-33.

Kim, D., Choi, I., Han, W., Ryu, Y., Kim, M. and Bae, C. 2013. Studies on HG type of *Heterodera glycines* in Korea. *Res. Plant Dis*. 19:31-35 (in Korean).

Kim, D. G., Riggs, R. D., Robbins, R. T. and Rakes, L. 1997. Distribution of races of *Heterodera glycines* in the Central United States. *J. Nematol*. 29:173-179.

Lee, G.-A., Crawford, G. W., Liu, L., Sasaki, Y. and Chen, X. 2011. Archaeological soybean (*Glycine max*) in East Asia: does size matter? *PLoS ONE* 6:e26720.

Liu, S., Kandoth, P. K., Lakhssassi, N., Kang, J., Colantonio, V., Heinz, R., Yeckel, G, Zhou, Z., Bekal, S., Dapprich, J., Rotter, B., Cianzio, S., Mitchum, M. G. and Meksem, K. 2017. The soybean *GmSNAP18* gene underlies two types of resistance to soybean cyst nematode. *Nat. Commun*. 8:14822.

Mitchum, M. G., Wrather, J. A., Heinz, R. D., Shannon, J. G. and Danekas, G. 2007. Variability in distribution and virulence phenotypes of *Heterodera glycines* in Missouri during 2005. *Plant Dis*. 91:1473-1476.

Niblack, T. L., Arelli, P. R., Noel, G. R., Opperman, C. H., Orf, J. H., Schmitt, D. P., Shannon, J. G. and Tylka, G. L. 2002. A revised classification scheme for genetically diverse populations of *Heterodera glycines*. *J. Nematol*. 34:279-288.

Noel, G. R. 1992. History, distribution, and economics. In: *Biology and management of the soybean cyst nematode*, eds. by R. D. Riggs and J. A. Wrather, pp. 1-13. The American Phytopathological Society, St. Paul, MN, USA.

Riggs, R. D. 1977. Worldwide distribution of soybean-cyst nematode and its economic importance. *J. Nematol*. 9:34-39.

Riggs, R. D. and Schmitt, D. P. 1988. Complete characterization of the race scheme for *Heterodera glycines*. *J. Nematol*. 20:392-395.

Sakai, H. and Kushida, A. 2019. Molecular confirmation of the occurrence of *Heterodera sojae* in Japan. *Nematol. Res.* 49:29-33.

Shaibu, A. S., Li, B., Zhang, S. and Sun, J. 2020. Soybean cyst nematode-resistance: gene identification and breeding strategies. *Crop J*. 8:892-904.

Turner, S. J., Stone, A. R. and Perry, J. N. 1983. Selection of potato cyst-nematodes on resistant *Solanum vernei* hybrids. *Euphytica* 32:911-917.

Tylka, G. L. 2016. Understanding soybean cyst nematode HG types and races. *Plant Health Prog*. 17:149-151.

Vanderplank, J. E. 1978. Genetic and molecular basis of plant pathogenesis. Springer-Verlag, Berlin, Germany. 167 pp.

Wang, J., Niblack, T. L., Tremain, J. A., Wiebold, W. J., Tylka, G. L., Marett, C. C., Noel, G. R., Myers, O. and Schmidt, M. E. 2003. Soybean cyst nematode reduces soybean yield without causing obvious aboveground symptoms. *Plant Dis*. 87:623-628.

Yokoo, T. 1936. Host plants of *Heterodera schachtii* Schmidt and some instructions. *Korea Agric. Exp. Stn. Bull.* 8:47-174.

Zhen, H., Peng, H., Kong, L., Hong, B., Zhu, G., Wang, R., Peng, D. and Wen, Y. 2018. *Heterodera sojae*, a new cyst nematode record in China and its parasitism to legume crops. *Sci. Agric. Sin.* 51:93-104.

Zheng, J., Li, Y. and Chen, S. 2006. Characterization of the virulence phenotypes of *Heterodera glycines* in Minnesota. *J. Nematol*. 38:383-390.