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Effects of Abiotic Environmental Factors on Soybean Cyst Nematode

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Abstract

As a pest, in order to complete its life history and reproduces effectively, soybean cyst nematode (SCN) (*Heterodera glycines* Ichinche 1952) must adapt to various environments and conditions for long periods of evolution. The nematode is widely dispersed year after year. Controlling this pest requires understanding characters and adaptability of SCN. Effects of abiotic factors, such as temperature, soil humidity, agrotype, pH value, ions, plant exudates, agricultural chemical and cultivation systems on SCN, are reviewed in this paper. The results show that SCN is able to endure various environmental stresses, especially low temperature. Because of its special life history, cyst stage help SCN over winter, resistance of SCN to environmental stress is strong. A few studies have reported the mechanism of SCN environmental adaptability. We emphasized the importance of studying environmental adaptability of SCN, which would benefit the control of SCN by ecological means.

Key words: soybean cyst nematodes (SCN), abiotic, environmental factors, ecological

INTRODUCTION

Nematodes are a diverse group of invertebrates (Robert 2003). More than 15 000 described species probably represent only a small portion of the total member in the phylum Nematoda (Barker and Koenning 1998). The soil is a particularly rich habitat for nematodes, with about 26% of described genera inhabiting soil as bacterivores, fungivores, omnivores, predators, or plant parasites (Wharton 2005). It is said that wherever there is soil there are nematodes. Soybean cyst nematode (SCN) can occur wherever there are soybeans. Most likely, SCN was first found in northeast China in 1899 (Dai 1958), and was first reported in 1915 by Japanese. Now, SCN is distributed in soybean planting areas all over the world. SCN is a small plant-parasitic roundworm that attacks the roots of soybeans, and becomes one of the most destructive pests of soybeans.

The SCN life cycle has three stages: egg, juvenile, and adult. Soybeans are infected by the second-stage juvenile - a microscopic (1/60th-inch long), colorless worm. Juveniles penetrate the soybean by puncturing the roots with a spear-like feeding structure, the stylet. They invade the root, then migrate toward food-conducting tissues, it is here that they feed and grow. Feeding causes changes of internal root structure, thereby interfering with normal root functions and ultimately causing plant damage. In approximately three weeks, under optimum conditions (soil temperatures at 27-29°C), juveniles grow into egg-bearing females.

The enlarged females become lemon-shaped. They break through the root surface while their heads remain attaching to the roots. The females lay eggs in a jellylike mass attached to their posterior end and retain about two-thirds of the eggs within their swollen bodies. Once

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they died, the white female stage changes to yellow, and then to brown cyst, which is a protective structure containing 200-400 eggs and protects the eggs from drying, chemical action, predators, and some parasites.

As a typical soil-borne pest, SCN is not only influenced by hosts, but also by environmental factors, such as temperature, soil moisture, agrotype, pH value, ions, plant exudates, agricultural chemical and cultivation systems. SCN is able to adapt to various environments and conditions. For instance, SCN are dormant in cysts withstanding temperature at -40°C or below to survive through long cold winter (Wu *et al.* 2006).

Our research on the response of SCN environmental adaptability generally has two goals. One goal is to quantify the relationships between various environmental conditions, especially extreme environmental conditions, and mortality for the purposes of understanding species distributions and population dynamics. The other goal is to describe and understand the life-history, behavioral, and physiological adaptations that permit this species to survive periods of extreme environmental conditions. These two goals are related in that knowledge of the adaptations evolved in SCN to survive extreme environmental conditions, which is critical for the development of ecologically relevant procedures for the accurate quantification of their limits of tolerance. This paper will focus primarily on effects of different abiotic factors on SCN. We believe in that ecological control systems against SCN will be established based on knowledge effects of environmental factors on SCN.

ADAPTABILITY TO ENVIRONMENTAL FACTORS

Temperature

Temperatures suitable to the development of nematodes, such as hatching, reproduction, movement and growth, are different between species and community. The temperature character of the same species is different if community is different (Liu 1998). There are 5 temperature stages affected plant nematodes: low lethal temperature, low non-lethal temperature, optimal temperature, high non-lethal and high lethal temperature (Liu 2000).

Normal temperature

SCN reproduces well under a broad range of temperatures and need different temperatures for each growing stages in its life history.

The relationship of temperature to SCN development from 15 to 30°C was described by a linear model. The optimum temperature of cyst's hatch is 24°C (Liu 2000). Thermal optimum for embryogenesis and hatch was 24°C (Alston and Schmitt 1988). From 14 to 36°C SCN J2 can infect hosts, and the optimum temperature is 18-25°C. Juveniles begin to decline when the temperature is higher than 31°C, furthermore, juveniles can't developed to adults when the temperature reaches to 35°C (Anand and Matson 1995). Eggs developed to first-stage juveniles at 10°C at lest and to second-stage juvenile at 15-30°C (Alston and Schmitt 1988). Hatch occurred at 20-30°C. Female adults lay eggs well at 23-28°C (Liu 2000). The growth rate and the temperature are positively correlated within the proper range of temperature, in other words the higher the temperature is, the more rapidly juveniles develop. This leads to a decrease days needed to go through one generation, which may result in large population of SCN.

Low temperature

SCN is widely distributed, mainly in cold regions. In order to have normal development and better existence, SCN must overcome the challenges of winter cold in the temperate and frigid areas.

SCN is able to endure possible low temperature of natural conditions, its eggs in cysts may survive more than 7 days at -40°C (Ichinohe 1955), and may survive more than 18 months at -24°C (Slack and Hamblen 1961). But larva can not survive at 0°C. During the dormancy stage, plant parasitic nematodes may tolerate low temperature, but during their active stages nematodes die at 0°C (Liu 1998).

Nematode's cold tolerance has mainly been divided into frigid tolerance and frigid avoidance. The mechanism of frigid tolerance is that nematodes can survive under freezing condition with water freezes extracellularly. Frigid tolerance is more widespread among nematodes than frigid avoidance. Frigid avoidance means that nematodes can avoid the formation of ice in their body fluids by means of getting super-cooling point down (Dai 2006).

Nematodes optimize their strategies in response to environmental changes. In different living periods, nematodes adopt different cold tolerance strategies. Generally, juveniles and adults adopt freezing tolerance strategies; moreover, some nematode and their eggs with sheath, such as SCN, adopt frigid avoidance. In addition, nematodes' cold tolerance varies with the environmental changes, and they may adopt the most optimized strategies (Wharton *et al.* 2005).

The nematodes' cold tolerance mechanisms contain forming particular growth stage, cold acclimation, collection of anti-freezing substances with low molecular weigh and macromolecular antifreeze proteins and heat shock protein. Eggs of SCN are protected by cysts in the soil in winter, in fact cyst stage is a particular stage of SCN life cycle. Most researchers find that nematodes' ability of cold tolerance is strengthened by cold acclimation. In addition, some anti-freezing substances, such as trehalose and glycerin, are produced and cumulated by cold acclimation (Grewal and Jagdale 2002). Trehalose is the most important antifreeze substance. It is able to stabilize protein structure when the environmental temperatures are low (Womersley 1981).

In recent years, various macromolecular proteins, such as ice-nucleating proteins (INPs), lipoproteins (LPs), and antifreeze proteins (AFPs) or thermal hysteresis proteins (THPs), have been found in a number of organisms. INPs and AFPs of nematodes have been studied already. It is estimated that there are INPs in bodies of frigid tolerant nematodes (Dai *et al.* 2006). Bodies of all organisms are induced to produce heat shock proteins (HSPs), when they are exposed to high temperature (sub-lethal temperature) or other stressful environments. HSPs are found in free nematodes and parasitic nematodes (Heschl and Baillie 1990; Martinez *et al.* 2001). But until now, the correlation between HSPs and cold tolerance ability is not clear.

Soil humidity

Water not only controls the whole life history of SCN, but is also an important medium for its movement. Water is indispensable for SCN, however humid soil may cause nematodes anoxia. It is well-known that SCN seriously infect soybean when the soil is dry. In other words, SCN have better strategies to survive desiccation rather than high humidity. When soil humidity is high, the proportion of white cysts decrease in soybean roots, and the hatch rate of juveniles is reduced. When relative soil humidity is 2-3%, juveniles in eggs can survive 5 months; juveniles inside cysts without soil can survive 2 months; juveniles in eggs can survive 1-4 days; and dissociative juveniles will die after 10 min (Liu 1998).

Agrotype

Jones and Thomasson (1976) believed in that nematodes inhabited interstices with diameters of over 30 μm, yet nematodes were not able to go through interstices which diameters were smaller than 30 μm. The size of interstices of soil granules differs in different types of soil. For instance, interstices of sandy soil are larger than those of clay (Jones and Thomasson 1976).

Soybean cyst nematode is influenced by soil structure in various degrees. Soil granules which diameter is 150-250 μm are avail to SCN's development (Liu 2000). The influence of soil type on SCN, is in the sequence of sand < loam < clay. In general, textures of sandy soil, dry land and hillock are loose, and SCN act easily, thus freely develop in these kinds of soil. Yang (1998) indicated that if soil contained more than 3% organic matter, the soybean yield was not seriously reduced, even if a few cysts inserted in the soybean plants (Yang *et al.* 1998). In Heilongjiang Province, China, SCN occurred heavily in brown soil and white slurry, which are sticky clay, while occurring lightly in meadow and swamp (Ji and Xu 1995), and SCN population were larger in saline alkali soil than in sandy loam (Liu *et al.* 1987).

pH value

Results of different studies looking at the influence of pH on plant parasitic nematodes are not consistent. Anand and Matson (1995) studied the stability of resistance to SCN of different soybean genotypes to various soil pH value and found that SCN reproduction was higher in pH 6.5 and 7.0 soil than that in pH 5.5 soil. In neutral soil, which pH value is 6.5, the

SCN population reached to the greatest. SCN reproduce more in moderate alkali soil than in moderate acid soil, but too alkali soils or too acid soils go against development of SCN (Yang *et al.* 1998; Wu *et al.* 1996). It is thought that higher pH values may be of benefit for the growth of soybeans, due to stronger development of roots, therefore, infection sites of SCN on soybeans increased (Anand and Matson 1995). Other reports showed that low pH value positively affected the foundation of a thick cork layer in soybean roots thus diminishing infection by nematodes (Ruan *et al.* 2002). On the other hand, conditions with low pH value (lower than 6) and high pH value (higher than 8) both inhibit growth of nematodes. Miller and Chen (2002) found that soil pH value was correlated with SCN egg density in the soil. The quantity of SCN reproduction in soil with pH 8.1 value was twice than that in soil with pH 5.5 (Miller and Chen 2002).

Ellenby (1945) reported that eggs were not able to hatch in buffer fluid of pH 3.4, but eggs hatched well at pH 6.0. When the pH value was reduced from 6.7 to 4.0, the hatch rate decreased (Ellenby 1945). Fenwick's (1951) study showed that the hatch rate didn't significantly differ between pH 3.0 and 8.0 (Fenwick 1951). It was thought that reproduction and hatch rate of *Globoder rostochiensis* in acidic soil were similar to those in alkaline soil. Mai and Harrison (1959) also believed that the pH value, which had no effect on potato growth, did not influence the infection of *G. rostochiensis* (Mai and Harrison 1959).

Our lab tested the adaptability of SCN J2 to 12 pH gradients which varied from pH 2 to 13. The result of this pH value assay indicated that SCN J2 mostly die when pH was 2 and 13; however, they could survive as long as pH value was between 4 and 11. Thus, we concluded that SCN J2, which could survive in highly acidic and alkaline environments, could adapt to a wide pH range (unpublished).

Ions

Behm *et al.* (1995) studied the hatch rate of SCN eggs after being treated *in vitro* with $ZnSO_4$ and $ZnCl_2$ solution, separately. The results of this study showed that after treated with $ZnSO_4$, the hatch rate of SCN was much higher than that treated with ion-free water, while $ZnCl_2$ solution inhibited hatch of SCN eggs. Compounds with Zn^{2+} can inhibit SCN egg hatching within *in vitro* experiment, but have no effect *in vivo* within natural soil (Behm *et al.* 1995). Other positive metal ions such as Cu^{2+}, Mn^{2+}, and Fe^{3+} also inhibit hatch of SCN eggs, and the higher the ionic concentration was, the stronger the inhibiting effect (Young 1999).

Researchers found that hatch of cyst nematode eggs depended on species of cyst nematodes and the kinds of ions present (Wallace 1956; Clark and Shepherd 1964).

Xing *et al.* (2002) reported that Zn^{2+} stimulated egg hatching whereas, Cu^{2+}, Mn^{2+} and Fe^{2+} had an inhibitory effect. The latter three ions also appeared to inhibit soybean seed germination and root growth. However, they did not continuously affect the growth of soybean throughout the lifecycle (Xing *et al.* 2002).

We tested the sensitivity of SCN J2 to ions (NO_2^-, NO_3^-, and NH_4^+) in nitrogenous solutions and compounds *in vitro*. The results indicated that the mortality was positively related to the increase of nitrogenous ions present. Furthermore, lower concentrations of N-NO_2^- was lethal to most of the tested SCN J2, and the lethal effect of urea took second place. Higher NH_4^+ and NO_3^- killed J2 of SCN. There is currently some uncertainty as to the mechanism by which NO_2^- kills nematodes. The most plausible mechanism is the generation of nitrous acid (HNO_2) by the association with hydronium ions (Zheng *et al.* 2007).

At present, the study of the toxicity of nematodes is limited to certain phenomena, such as testing mortality of larva and hatch rate of eggs, but does not investigate the ion toxicity mechanism in nematodes. However, many researches of toxicity mechanism of ions (especially metal ions) about other small lower animals such as earthworm, fish, shrimp, tadpole, and so on, have been reported.

Plant exudates

Plant exudates play an important role in egg hatching. Before nematodes hatch, chemical components of hosts' root exudates are bound to interact with the parasitic nematodes and some may inhibit egg hatching.

Component of plant exudates

Plant exudates are chemical substances that are released into the soil by different parts of the plant roots. There are four types of root exutes: (1) exudates: components of small molecular weight transuding passively from root cells; (2) secretions: substances releasing initiatively during metabolism; (3) adhesive gelatinousness and exfoliation exudates: root cap cells, substances and debrids exfoliating from roots and surface cells without secondary cell wall; (4) exudates resulting from the decomposition of root residues (Wang *et al.* 1995).

Exudates of healthy integrate roots contain many substances, such as glusides (over 10 kinds), amino acids (over 120 kinds), organic acids (over 10 kinds), vitamins (over 10 kinds), nucleotides (4 kinds), 4 kinds of hatching agents, 2 kinds of nematode attractants and various other compounds (over 10 kinds) (Zhang *et al.* 1992). So, it concluded that effective root exudates, which stimulate hatch of eggs, may contain some hatch agents. Root exudates of soybean are generally flavones, flavonoids and phenol substances (Yan *et al.* 1998). Root exudates contain 2 kinds of flavonoids substances, which induce reproduction and location of soybean rhizobium (d'Arcy-Lameta and Jay 1986). Masamuni *et al.* (1982) obtained glycinoeclepin A, which stimulated SCN eggs' hatch, from root exudates of kidney bean and other legume crop.

Effects of plant exudates on nematodes

Plant exudates are important factors that affect the hatching of SCN eggs. Generally, compared with those from many non-hosts, exudates from host plant roots may have more effects on the hatching of SCN eggs according to *in vitro* experiments (Schmitt *et al.* 1991). However, many researches showed that exudates of some non-host plants also stimulated hatching of SCN.

Plant residues from nonhosts [*Lespedeza capitata* Michx, *Lespedeza intermedia* (S. Wats.) Britt, *Lespedeza hirta* (L.) Hornem, *Lolium multiflorum* Lam., *Lolium perenne* L., *Lupinus perennis* L., *Melilotus officinalis* (L.) Lam., *Medicago sativa* L., *Trifolium pratense* L., Fairway B Lawngrass mixture, and *Pisum sativum* L.] reduced the number of SCN juveniles in the soil prior to planting soybeans and subsequently in the roots of soybeans. *L. multiflorum* was the most effective of the species tested in reducing the populations of SCN. Root exudates of nonhosts [*L. capitata*, *Trifolium hybridum* L., *Trifolium repens* L., *L. multiflorum*, *L. sperennis*, *Echinochloa crusgalli* (L.) Beauv., *Vicia villosa* (Roth), and *M. sativa*)], and of the host *G. max* increased the hatching rate of SCN egg in comparison to the water control. These plants' exudates increased neutral lipid utilization of SCN juveniles (Riga *et al.* 2001).

Root exudates of soybean and *E. crusgalli* (L.) Beauv could accelerate hatching of SCN eggs, and root exudates of durra, maize and cotton inhibit hatching (Yang 1984). Xu *et al.* (2004) studied the effects of root exudates of 5 northern crops, such as soybean, maize, wheat, flax and sugar beet, from different rotation systems on SCN eggs hatching. The results showed that root exudates of these 5 crops stimulated hatching of SCN eggs in the following sequence: sugar beet>maize >soybean>flax>wheat. Both the effects of the same crops from different rotation systems on hatch and the effects of different crops from the same rotation systems on hatch appeared to differ (Xu *et al.* 2004).

The effects of different soybean cultivars on SCN egg hatching are different. For example, the SCN hatching stimulating activity of root exudates of susceptive soybean cultivars, is higher than those of exudates of resistant soybean cultivars. Root exudates from the Lee soybean cultivar, which is SCN susceptible, were shown to stimulate egg hatching, unlike those of the Peking cultivar, which is a resistant cultivar (Liu *et al.* 1993). Si *et al.* (2004) reported that exudates from Kangxian 3 cultivar roots inhibited SCN egg hatching, while root exudates of the Hefeng 25 cultivar accelerated egg hatching. Root exudates of the Kangxian 4 cultivar had no significant effect on hatching of SCN eggs, neither inhibitory nor stimulator (Si *et al.* 2004). Two possible reasons explaining the stimulation of egg hatching by root are SCN eggs are directly stimulated by root exudates or increase in the permeability of cysts to root exudates (Yan *et al.* 1997).

Pesticide

Until recently, nematodes had been essentially ignored with respect to a general capacity to adapt to nematicides and other forms of environmental stress (David 1990). David (1990) put forward that behavioral modification of nematodes subject to long-term stress with non-fumigant nematicides (NFN) is a complex phenomenon, rather than a simple development of pesticide resistance (David 1990). Early warnings with respect to the potential of nematodes to develop resistance to nematicides beginning some decades ago with plant parasitic nematodes were generally ignored (Trujillo-Alvarado 1956). But now there is abundant evidence that nematode populations adapt to nematicides and other forms of environmental stress as do most other organisms (Viglierchio and Brown 1989).

Besides resistance of SCN to nematodes, environment safety and high cost of nematicides are other problems in soybean production. So nematicides are not applied to soybean production.

Herbicides are used frequently in soybean fields in China. Varieties of herbicides are sprayed during soybean growth periods. Not only herbicides have effects on weeds, but also on SCN through many experiments and surveys. Application of acifluorfen, bentazon, and lactofen to foliage of soybean plants inhibited hatching of SCN eggs from the same plants (Levene *et al.* 1998a). Crop oil concentrate (COC), and nonionic surfactant (NIS) applications also reduced SCN egg population densities by 50 to 60% compared with the untreated control 4 and 8 weeks after application. Treatments reduced SCN reproduction only when applied to soybeans and had no effect on SCN reproduction when applied directly to the soil (Levene *et al.* 1998b). Wong (1993) tested effects of eight herbicides, which were atrazine (atrazine), basagran (bentazon), bladex (cyanazine), blazer (acifluorfen), command (clomazone), lasso (alachlor), sonalan (ethalfluralin), and treflan (trifluralin) on *in vitro* hatching of SCN. Compared with deionized water, Blazer reduced hatching of SCN eggs, but the specific component of Blazer inhibiting egg hatching is unknown. Other herbicides tested at various concentrations had no significant effect on egg hatching. Suppression of hatching by Blazer indicates that this post-emergence soybean herbicide may have a potential role in managing SCN (Wong *et al.* 1993).

Tillage system

Crop rotation is a common mean of reducing pathogen populations in soil. Many rotation crops have been shown to reduce SCN populations (Weaver *et al.* 1998). For example, Sunn hemp (*Crotalaria juncea*), forage pea (*Pisum sativum*), lab-lab bean (*Lablab purpureus*), Illinois bundleflower (*Desmanthus illinoensis*), and alfalfa (*Medicago sativa*) generally resulted in smaller egg population density in soil or number of cysts formed on soybean than the fallow control in a greenhouse screening study (Warnke 2006). Velvetbean and bahia grass as rotation crops reduced population density of SCN to planting soybean (Warnke 2006). Population of SCN cyst also reduced in long-term rotation cultivation of wheat-wheat-soybean-rape-corn-soybean, and reached to homeostasis after rotation for a long term (Jin 2006). In Minnesota, the lowest densities of SCN eggs were typically found in cropping sequences that involved continuous maize (Porter *et al.* 2001). Therefore, inclusion of corn into a cropping sequence is a much more valuable SCN management tool (Creech *et al.* 2008).

Koenning *et al.* (1995) found that population densities of SCN were greater in conventionally tilled plots than in no-till plots. SCN population densities declined in a predictable manner when a non-host was planted (Koenning *et al.* 1995).

Generally the population density of SCN was more in continuous cropping than rotation. In north China, the number of SCN including the number of cysts and all juveniles of different stages in soil and roots of soybeans was notably increased under continuous cropping soybean field against under rotation (Chen *et al.* 2007).

It is interesting that the situation changes during long-term continuous crops. Quantity of SCN cyst decreased rapidly in the first 3 years under continuous cultivation of wheat or corn. After 4 years, the reduction became slower, and SCN cysts in the soil were very few, after 14 years. It is prevalent that diseases of plant parasitic nematodes naturally degenerate. The phenomenon is that if one susceptive cultivar is continuously cultivated in one field for many years (at least 5 years), the former serious nematode disease will disappear suddenly or will greatly lighten. So far, this phenomenon has been found in at least 9 kinds of cyst nematode disease (Jin *et al.* 2006).

CONCLUSION

Soybean cyst nematode disease is epidemic and destructive. Distributed widely, seriously disserving and wide approach of spreading are characters of this disease. As a soil-borne disease it is very difficult to control. Now breeding resistant cultivars is a main management to control SCN. But its shortcomings are still obvious, such as long period of breeding resistant cultivars, resistance being easily to lose and so on (Yu 1998). Because the large demands of soybean yields in China, rotation with other crops is not a feasible method to control SCN, although rotation is effective and safe. There is no effective, economical and safe management to control SCN, now.

Any species exists in the earth reproducing generation by generation by continuous evolvement in varying environments which it gradually adapts to. "All that is real is rational, and all that is rational is real". The long-time existence of soybean cyst nematode is the result of adapting to environment.

SCN live in environment of soybean agricultural ecological system. In the system, SCN not only need to adapt to different seasons and other organism in soil, but also need to adapt to influences on their living environment brought by behaviors of human being, such as planting different cultivars, adopting different cultivation system and application of agrochemicals and so on.

It is worthy of studying on effects of various conditions on SCN, and mechanism of adaptability. That is helpful to control the disease. After experiencing tortuosity, plant pathologists are clear about that diseases are not possible and necessary to be destroyed at all. Because some quantity of pathogens are helpful to maintaining balance of environment, and are not seriously harm to crops. The aim to study on effects of environmental factors is to probe how to control SCN from the ecological angle. We expect to control the quantity of SCN under the precondition that the environment is not been destroyed. We assume to manage those processes scientifically, such as seeding, fertilizing, irrigating, cultivation system and so on. We also assume to change soil environment to control the quantity of SCN, by means of combing fertilizer and microorganism preparation and applying them to soil quantitatively at proper time. Certainly this technology is difficult to application, especially in the soil where ecological balance has been destroyed. Besides, soybean is field crop, so maneuverability of SCN ecological control is not clear yet. It's necessary for us to study on it further.

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