POPULATION DYNAMICS OF *GLOBODERA PALLIDA* UNDER POTATO MONOCULTURE

C. Eberlein[1], H. Heuer[2], S. Vidal[3], and A. Westphal[4]*

[1]Institute for Plant Protection in Field Crops and Grassland, Julius Kühn-Institut, D-38104 Braunschweig, Germany; [2]Institute for Epidemiology and Pathogen Diagnostics, Julius Kühn-Institut, D-38104 Braunschweig, Germany; [3]Department of Crop Sciences, University of Göttingen, 37077 Göttingen, Germany; [4]University of California Riverside, Department of Nematology, Kearney Agricultural Research and Extension Center, Parlier, CA 93648, USA *Corresponding author: andreas.westphal@ucr.edu.

ABSTRACT

Eberlein, C., H. Heuer, S. Vidal, and A. Westphal. 2016. Population dynamics of *Globodera pallida* under potato monoculture. Nematropica 46:114-120.

Globodera spp. are under strict quarantine in many countries. Quarantines can hamper international trade, restrict the exchange and transport of agricultural goods, and require comprehensive in-state regulatory efforts. Often, the development of soil suppressiveness to cyst nematodes under monoculture of susceptible hosts is observed. In this research, the development of soil suppressive to *Globodera pallida* was evaluated over a 5-yr monoculture of susceptible potato in soil infested with *G. pallida* Pa3. Microplots infested with cyst nematode populations "Chavornay" or "Delmsen" were continuously cropped with susceptible potato 'Selma'. Final cyst populations did not increase from 2010 to 2014. Final populations of total eggs remained similar for Delmsen but oscillated for Chavornay. This dynamic was also observed in the multiplication rate of cysts and total eggs of both nematode populations. Multiplication rates of cysts decreased by 60% for the Delmsen population. In both nematode populations, final proportions of diseased eggs increased in 2010 and oscillated until 2014, especially for Chavornay. This suggested a predator-prey relationship of the nematode and a suppressive factor. Yields of total marketable potato tubers increased in Chavornay but decreased in Delmsen. In this first report, numerical changes of cysts and diseased and healthy eggs of *G. pallida* under a potato monoculture were monitored. It remained unclear if organisms interfered with nematode activity, and if these could be beneficial in reducing the risk for nematode damage in potato production.

Key words: *Globodera pallida*, population dynamics, potato monoculture, suppressive soil.

RESUMEN

Eberlein, C., H. Heuer, S. Vidal, A. Westphal. 2016. Dinámica poblacional de *Globodera pallida* en un monocultivo de papa. Nematropica 46:114-120.

Globodera spp. se encuentra bajo cuarentena estricta en muchos paises. Las medidas de cuarentena afectan al comercio internacional, restringen el intercambio y transporte de productos agrícolas y requieren esfuerzos exhaustivos por parte de las autoridades estatales. Frequentemente, se observa desarrollo de supresividad a nemátodos quísticos en suelos que se encuentran bajo el monocultivo de hospederos susceptibles. En este estudio se evalua el desarrollo de supresividad a *Globodera pallida* durante un monocultivo de 5 años de papa susceptible en un suelo infestado con *G. pallida* Pa3. Cuando microparcelas infestadas con las poblaciones Chavornay o Delmsen fueron cultivadas continuamente con la variedad de papa susceptible 'Selma', las poblaciones de quistes no aumentaron desde el año 2010 al año 2014. Las poblaciones finales de huevos permanecieron similares para Delmsen, pero oscilaron para Chavornay. Esta dinámica también fue observada en la tasa de multiplicación de quistes y huevos totales de ambas poblaciones de nemátodos. La tasa de multiplicación de quistes decreció en un 60% para la población de Delmsen. Para ambas poblaciones de nemátodos, las proporciones finales de huevos enfermos mostraron un pronunciado aumento en el año 2010 y oscilaron hasta el año 2014, especialmente para Chavornay. Esto sugiere una relación de predador-presa sobre el nemátodo y un factor supresivo. La producción comercializable de papas aumentó en Chavornay pero decreció en Delmsen. En este primer reporte, se monitorearon las fluctuaciones en el número de quistes, y de huevos sanos y enfermos de *G. pallida*, bajo un monocultivo de papas. Aun no queda claro si hubo una interferencia de organismos con la actividad de los nemátodos, y si acaso éstos pudiesen ser beneficiosos en reducir el riesgo de daño causado por este nemátodo en la producción de papas.

Palabras clave: Globodera pallida, monocultivo de papa, dinámica poblacional, suelo supresivo.

INTRODUCTION

Worldwide, potato (*Solanum tuberosum* L.) serves not only as one of the most important vegetable crops but also provides renewable raw material, e.g., for the production of starch (FAO, 2008). Potato cyst nematodes (PCN; *Globodera pallida* (Stone) Behrens and *G. rostochiensis* (Wollenweber) Behrens) strongly limit productivity of potato (Scurrah *et al.*, 2005). This severe damage potential of *Globodera* spp., resulted in the classification of PCN as quarantine pests in the European Union, the Asia and Pacific Plant Protection Commission (APPPC), and the North American Plant Protection Organization (NAPPO; CABI/EPPO, 1997). Legislative control measures are in place to contain the spread of these pests (European Union, 2007). In Europe, fields must be checked for and found to be free of infestations with *Globodera* spp. prior to production of seed potatoes. In the presence of *Globodera* spp., cropping nematode-resistant cultivars of consumption potatoes may be prescribed by the local plant protection service.

Common nematode management strategies are difficult to implement. For example, crop rotations of non-hosts would need to be excessively long because of the very low decline rates of *G. pallida* (Evans and Haydock, 2000). A number of cover crop options are being explored, but the effectiveness of these in suppression of nematodes is unclear. The use of *Solanum sisymbriifolium* Lam has been demonstrated to reduce PCN in the Netherlands (Scholte, 2000). More recently, brassica cover crops were found to reduce population densities by biofumigation (Ngala *et al.*, 2015). Due to their costs, toxicology, or because they have been banned from the market, only a limited number of fumigants and non-fumigant nematicides have been used commercially against *Globodera* spp. In Germany as of 2014, only the nematicide, fosthiazate, is registered in potato. It may protect yields, but it does not decrease numbers of *Globodera* spp. during the crop cycle (Woods *et al.*, 1999). Thus, this material does not fulfil the regulatory requirement of nematode reduction to be a permitted management strategy, and may not be used as fulfilment of the mandatory management requirement.

In light of these limited strategies, potato production systems depend on the use of resistant cultivars. The usefulness of resistant cultivars is limited by the number of cultivars available against *Globodera* species and pathotypes (CABI/EPPO, 1997). The evolution of new pathotypes, together with the selection of nematode populations that are not controlled by the frequently used H_1 gene of resistance to *G. rostochiensis*, may result in a shift in pathotype or nematode species (Schouten and Beniers 1997; Evans and Haydock, 2000). Based on these challenges, additional management strategies are urgently needed.

Potato cyst nematodes (PCN), like other nematodes, inhabit the complex environment of the soil where they are in constant interaction with potentially antagonistic microorganisms found in undisturbed soils or in soils with continued cropping of susceptible hosts (Stirling, 1991; Westphal, 2005). The current view is that monoculture of susceptible host plants of the specific nematode pest is a prerequisite for the development of suppressive soil (Gair *et al.*, 1969). Several cyst nematode-suppressive soils have been reported (Kerry and Crump, 1998; Westphal and Becker, 1999; Westphal and Xing, 2011). In these induced suppressive soils, continuous increase of the primary parasite, the nematode, was followed by a build-up of antagonists that then reduced nematode reproduction. In cereal cyst nematode in the UK, the parasitic fungi, *Nematophthora gynophila* and *Pochonia chlamydosporium* (syn. *Verticillium chlamydosporium*), kept the nematode below economic threshold levels (Kerry *et al.*, 1982). In another agricultural cropping system, *Brachyphoris* (syn. *Dactylella*) *oviparasitica* was the key player in suppressiveness against *Heterodera schachtii* Schm. in California (Borneman and Becker, 2007). In comparison, limited research efforts have focused on suppressive soils against *Globodera* spp. (Roessner, 1987; Crump and Flynn, 1995).

The objectives of the current study were to test whether continued culture of susceptible potato leads to suppressiveness of the soil against *G. pallida*, and how such culture would impact the health status of the nematode. Numbers of cysts, total and diseased eggs of two populations of *G. pallida* under potato monoculture were monitored.

MATERIALS AND METHODS

The experiments were conducted in microplots of 1 m^2 surface area containing sandy soil (90.0% sand, 5.4% silt, 2.4% clay, 2.2% O.M., pH 6.2). These plots had been originally infested with *G. pallida* Pa3, populations of two different origins: Chavornay and Delmsen, and used for different nematode management studies. For both nematode populations, replicate plots were available constituting two experiments (Chavornay: four replications; Delmsen: three replications). In April 2010, microplots with the Delmsen population were treated with Dazomet at 500 kg/ha (Tetrahydro-3,5-dimethyl-1,3,5-thiadiazine-2-thione; Basamid, BASF, Ludwigshafen, Germany), whereas plots

with Chavornay were left non-treated. The biocide treatment was applied as previous studies had shown that such treatment rendered field soil conducive to *Heterodera glycines* (Xing and Westphal, 2006). Here, it was used to perturb microbial populations. Every year prior to planting, plots were fertilized with varying combinations of calcium ammonium nitrate and multi-nutrient NPK fertilizer to deliver 54 to 120 kg/ha N, 30.6 to 34.9 Kg/ha P, and 132.8 Kg/ha K in support of optimum plant growth. Sprouted tubers of potato 'Selma', susceptible to populations of *G. pallida*, were planted to two evenly spaced parallel ridges at a total of six plants per microplot. Plants were maintained following standard regional cultivation recommendations including watering as

needed and fungicide applications for suppression of potato late blight, *Phytophthora infestans* (Mont.) de Bary. At harvest, potato tubers were dug, washed, and weighed. Fresh weights of marketable and total tubers were determined. Additionally, potato tubers were graded into diameter classes: < 30, 31-35, 36-55, and >55 mm.

To determine initial and final population densities of *G. pallida*, twelve 2-cm diameter cores of soil were collected per plot from the upper 30 cm prior to planting and after harvest from the plot area where the root zone of the potatoes was. Subsamples of 400 g of soil were used for extracting cysts by density centrifugation with $MgSO_4$ (Müller, 1980). Cysts were counted using a dissecting microscope before being crushed in a custom-made tissue grinder to release the eggs and juveniles. These were suspended in water and counted under an inverted transmitted light microscope (63 × magnification). Eggs and juveniles were classified into diseased (abnormal development or obviously colonized by microbes) or healthy (normally developed, intact J2 inside). Population densities of cysts and eggs were reported per 100 g of soil.

Data analysis

Analyses of variance were conducted in GLIMMIX procedure of SAS (version 9.3, SAS Institute, Cary, NC, USA). Data, including the independent variables nematode population and year, and the response variables related to the initial and final population densities of cysts and eggs and yield parameters, were analyzed as repeated measures. Statistical significance was set at $P \leq 0.05$. Results are presented as backtransformed lsmeans ± lsmse.

RESULTS

In *G. pallida* Chavornay, final population densities of cysts slightly increased from 2012 (160.2 ± 30.0) to 2014 (230.3 ± 43.0; $P = 0.04$; Fig. 1a). In Delmsen, final population of cysts decreased by 40% from 2010 to 2012 ($P < 0.01$), and then slightly increased from 2012 (105.6 ± 23.0) to 2014 (177.2 ± 38.3; $P = 0.02$; Fig. 1a). As a result, no significant increase was observed from 2010 to 2014 ($P = 0.81$). Final population densities of total eggs oscillated with large amplitudes in Chavornay, increasing 4.8-fold from 2010 to 2013 ($P < 0.01$), and then decreasing by 50% from 2013 to 2014 ($P = 0.01$; Fig. 1b). In Delmsen, final population of total eggs did not change significantly between 2010 and 2014 (Fig. 1b). A pronounced unusual seasonal increase of 35.8- and 26.7-fold in the proportion of diseased
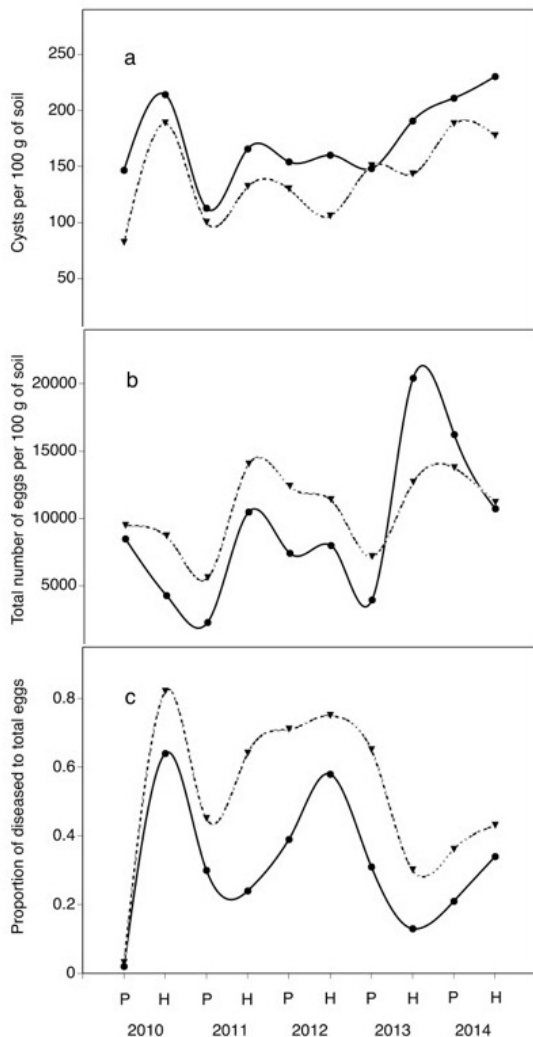

Fig. 1. Population densities of *Globodera pallida* Chavornay (●) and Delmsen (▼) on susceptible potato 'Selma' in monoculture (a) number of cysts, (b) number of total eggs, and (c) proportion of diseased eggs of total eggs. Population densities determined at planting (P) and harvest (H) each year.

eggs was observed from planting to harvest in 2010 for Chavornay and Delmsen, respectively (Fig. 1c). In Chavornay, cyclic oscillations were observed in final proportion of diseased eggs, which decreased from 2010 to 2011 ($P < 0.01$), then increased to 2012 ($P < 0.01$), decreased again in 2013 ($P < 0.01$) and eventually increased in 2014 ($P = 0.02$; Fig. 1c). In Delmsen, final proportion of diseased eggs remained similar until 2012, and then decreased until 2014 ($P < 0.01$; Fig. 1c). The multiplication rate (P_f/P_i) for cysts in Chavornay declined from 2011 (1.5 ± 0.2) to 2012 (1.1 ± 0.2; $P = 0.05$), and thereafter remained similar until 2014. In Delmsen, the multiplication rate of cysts decreased from 2010 (2.6 ± 0.4) to 2014 (1.1 ± 0.2; $P < 0.01$). The multiplication rate (P_f/P_i) of total eggs in Chavornay oscillated in a cyclic manner during the evaluated

period. It increased from 2010 (0.5 ± 0.2) to 2011 (4.6 ± 0.7; $P < 0.01$), then decreased to 2012 (1.1 ± 0.2; $P < 0.01$), increased again in 2013 (5.2 ± 0.7; $P < 0.01$), and eventually decreased in 2014 (0.7 ± 0.2; $P < 0.01$). For Delmsen, the multiplication rate of total eggs increased from 2010 (1.0 ± 0.3) to 2011 (2.7 ± 0.5; $P < 0.01$), and then declined to 2014 (0.9 ± 0.3; $P < 0.01$). A positive correlation between initial densities of healthy eggs and final densities of diseased eggs was found for Chavornay ($r = 0.46$, $P = 0.04$), whereas a positive correlation between final densities of diseased eggs and final densities of total eggs was found for Delmsen ($r = 0.73$, $P < 0.01$; data not shown).

Fresh weight of total marketable potato tubers per plant in Chavornay increased 2.7-fold from 2010 to 2013 ($P = 0.02$) and then remained similar until 2014 (Fig. 2). In Delmsen, total marketable potato tubers per plant decreased by 80% from 2010 to 2014 ($P < 0.01$; Fig. 2). In Chavornay, fresh weight of potato tubers per plant < 30-mm size increased 3.1-fold from 2010 to 2014 ($P < 0.01$; Fig. 3a). In Delmsen, this tuber category increased 3.0-fold from 2010 to 2013 ($P < 0.01$) and then decreased by 60% from 2013 to 2014 ($P = 0.04$; Fig. 3b). Potato tuber yield per plant 31-35 mm in Chavornay significantly increased 3.5-fold from 2010 to 2013 ($P = 0.02$), but decreased by 60% from 2013 to 2014 ($P = 0.05$; Fig. 3a). In Delmsen, this tuber category remained similar between 2010 and 2013 and decreased 70% from 2013 to 2014 ($P = 0.04$; Fig. 3b). Yield per plant 36-55 mm did not change significantly in Chavornay and Delmsen (Fig. 3a,b). Yield per plant >55 mm was only obtained in 2012 in one replicate of Chavornay (1.7 ± 1.0), and only registered in 2010 in Delmsen (172.8 ± 73.1; Fig. 3b).
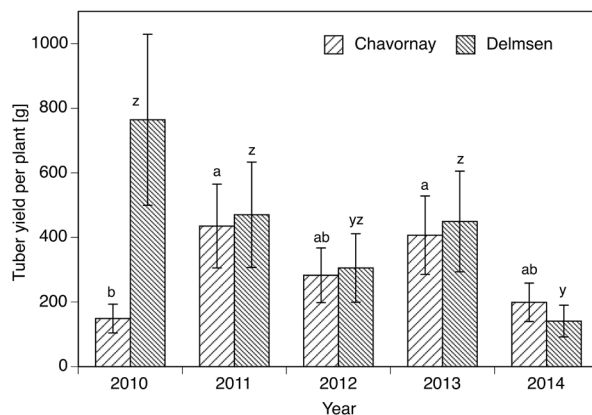

Fig. 2. Tuber yield of potato 'Selma' in monoculture plots infested with *Globodera pallida* Pa3 populations Chavornay or Delmsen (lsmeans ± lsmse) in years 2010 to 2014. Bars indexed with the same letter were not significantly different at $P = 0.05$; Chavornay: a,b; Delmsen: z,y.
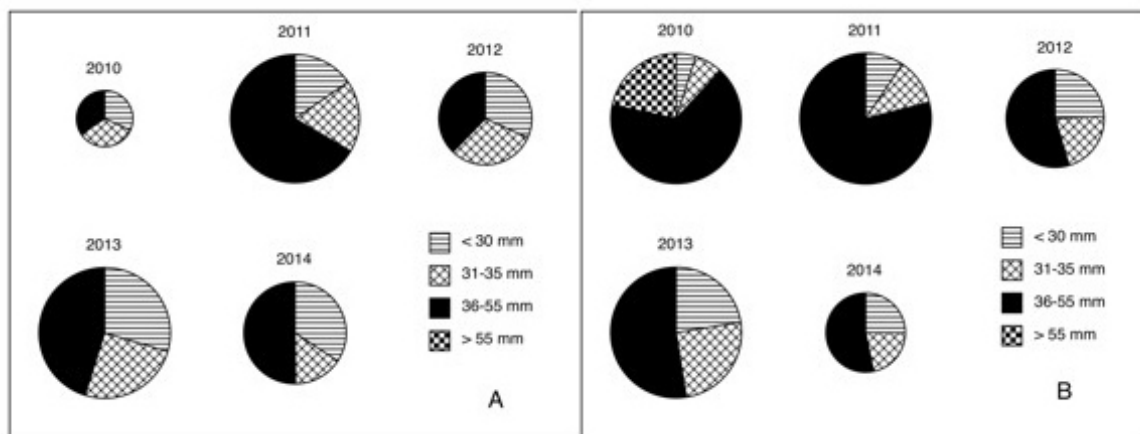

Fig. 3. Relative proportions of potato tuber size classes in *Globodera pallida* Pa3-infested plots of nematode populations (A) Chavornay and (B) Delmsen in years 2010 to 2014.

DISCUSSION

Under this 5-yr monoculture of susceptible potato, *G. pallida* egg populations became diseased, and egg numbers oscillated in a cyclic manner. This suggested density-dependent regulation of nematodes and their antagonists. There was no pronounced and continuous decline of the population densities of *G. pallida*, as had been observed in some other suppressive soil systems but many members of the nematode population became diseased. Full expression of suppressiveness may take longer to fully develop than was monitored in the current project.

A large increase in numbers of diseased eggs, especially in Delmsen population was observed in 2010 and also in 2012. Diseased eggs exhibited fungal hyphae or physiologically disordered content. Diseased eggs of unknown etiology were described by Tribe (1977) as oily degenerated, lysed, shriveled, coagulated, or decayed. Bursnall and Tribe (1974), Morgan-Jones *et al.* (1981) and Dackman (1990), who also found high proportions of these eggs, proposed that this disorder was caused by fungal metabolites or depletion of oxygen by fungi growing in the cyst, or even viral infections.

Fluctuations showing a cyclic behavior, with increases followed by decreases, were also reported by Heijboek (1983), in long-term observations of *H. schachtii* population densities under a sugar beet monoculture. These population dynamics may indicate a density-dependent predator (parasite) - prey (host) interaction (Lotka, 1925; Volterra, 1926) where a stabilizing effect should be expected, as antagonists destroy an increasing proportion of the prey (host) population as their abundance increases. However, the pronounced increase of healthy eggs in 2013 for Chavornay, exceeded the amplitude of previous fluctuations. This observation differs from those by Heijbroek (1983) who detected oscillations not significantly different from the tolerance limit that never reached the initial maximum density. As in most natural populations, these oscillations may be shaped by a combined action of density-dependent, density-proportional, and density-independent forces. Large oscillations occur where density-dependent actions are ineffective (Odum, 1954), but, in contrast, the predominance of density-dependent factors should lead to stability. We speculate that the experiment did not cover a sufficiently long period allowing a final decline of the nematode populations under this potato monoculture. Population densities can be maintained at equilibrium levels for several years, as has been seen under different monocultures of cysts nematodes (Gair *et al.*, 1969; Thielemann and Steudel, 1973; Heijbroek, 1983; Westphal

and Becker, 1999; Noel and Wax, 2003). In these studies, the number of cropping periods necessary for the decline of cyst nematode populations ranged from three to several more years (Gair *et al.*, 1969; Thielemann and Steudel, 1973; Kerry *et al.*, 1982; Heijboek, 1983; Westphal and Becker, 1999). Perhaps the number of generations that a nematode completes during one growing season is more important than the number of years for the population density decline. For example, nematodes like *Heterodera schachtii* or *H. glycines* that complete more than one generation per year (Thomason and Fife, 1962) may decline quicker than nematodes that have a single generation per growing period. The biocidal pre-plant treatment that was aimed at perturbing soil microbial communities did not seem to impact the development of high levels of diseased eggs.

When compared to other long-term experiments with *G. rostochiensis* under susceptible potato monocultures, the increase of our populations (eggs g^{-1} soil) from the first to the fourth year; 4.1-fold for Chavornay and 1.4-fold for Delmsen (first to fifth year: Chavornay: 2.2-fold; Delmsen: 1.3-fold) are similar to the increases found by Jones and Parrot (1969) in the UK (first to fourth year: 1.9-fold; first to fifth year: 1.3-fold), and below increases found by Zawiślak *et al.* (1989) in Poland (first to fourth year: 245-fold; first to fifth year: 1000-fold) and by Tiilikkala (1991) in Finland (first to fourth year: 2650-fold; second-stage juveniles g^{-1} soil). Interestingly, in the monocultures of Tiillikala (1991) and Jones and Parrot (1969), the densities decreased after the fourth year, with fluctuations becoming smaller with repeated cropping, tending to an equilibrium at which an intermediate root size was balanced by an intermediate population density (Jones and Parrot, 1969).

Findings of this study present baseline data for the dynamics of *G. pallida* under monoculture conditions. The monoculture did not lead to a severe and persistent decline as reported for other cyst nematode-suppressive soils. However, many members of the nematode population became diseased and a decline of the overall damage caused by this parasite was surmised. In a companion study, the microbial colonization of the cysts was further examined (Eberlein *et al.*, 2016).

ACKNOWLEDGMENTS

LITERATURE CITED

Borneman, J., and J. O. Becker. 2007. Identifying microorganisms involved in specific pathogen suppression in soil. Annual Review of Phytopathology 45:153-172.

Bursnall, L. A., and H. T. Tribe. 1974. Fungal parasitism in cysts of Heterodera II. Egg parasites of *H. schachtii*. Transactions of the British Mycological Society 62:595-601.

CABI/EPPO. 1997. Data sheets on quarantine organisms: *Globodera rostochiensis* and *Globodera pallida*. Pp. 601-606 *in* I. M. Smith, D. G. McNamara, P. R. Scott, M. Holderness, and B. Burger (eds.). Quarantine Pests for Europe. Wallingford, UK: CAB International.

Crump, D. H., and C. A. Flynn. 1995. Isolation and screening of fungi for biological control of potato cyst nematodes. Nematologica 41:628-638.

Dackman, C. 1990. Fungal parasites of the potato cyst nematode *Globodera rostochiensis*: Isolation and reinfection. Journal of Nematology 22:594-597.

Eberlein, C., H. Heuer, S. Vidal, and A. Westphal. 2016. Microbial communities in *Globodera pallida* females raised in potato monoculture soil. Phytopathology 106:581-590.

European Union. 2007. Council Directive 2007/33/EC of 11 June 2007 on the control of potato cyst nematodes and repealing Directive 69/465/EEC. Official Journal of the European Union L 156:12-22.

Evans, K., and P. P. J. Haydock. 2000. Potato cyst nematode management – present and future. Aspects of Applied Biology 59:91-97.

FAO. 2008. International Year of the Potato. Food and Agriculture Organization of the United Nations (FAO). Online. http://www.fao.org/potato-2008 (accessed 12.05.2014).

Gair, R., P. L. Mathias, and P. N. Harvey. 1969. Studies of cereal nematode populations and cereal yields under continuous or intensive culture. Annals of Applied Biology 63:503-512.

Heijbroek, W. 1983. Some effects of fungal parasites on the population development of the beet cyst nematode (*Heterodera schachtii* Schm.) Mededelingen Faculteit van de Landbouwwetenshappen Rijksuniversiteit Gent 48:433-439.

Jones, F. G. W., and D. M. Parrott. 1969. Population fluctuations of *Heterodera rostochiensis* Woll. when susceptible potato varieties are grown continuously. Annals of Applied Biology 63:175-181.

Kerry, B. R., D. H. Crump, and L. A. Mullen. 1982. Studies of the cereal cyst-nematode, *Heterodera avenae* under continuous cereals, 1975-1978. II. Fungal parasitism of nematode females and eggs. Annals of Applied Biology 100:489-499.

Kerry, B. R., and D. H. Crump. 1998. The dynamics of the decline of the cereal cyst nematode, *Heterodera avenae*, in four soils under intensive cereal production. Fundamental and Applied Nematology 21:617-625.

Lotka, A. J. 1925. Elements of Physical Biology. Baltimore, MD, USA: Williams & Wilkins.

Morgan-Jones, G., B. O. Gintis, and R. Rodriguez-Kabana. 1981. Fungal colonization of *Heterodera glycines* cysts in Arkansas, Florida, Mississippi, and Missouri soils. Nematropica 11:155-163.

Müller, J. 1980. Ein verbessertes Extraktionsverfahren für *Heterodera schachtii*. [An improved method for the extraction of *Heterodera schachtii*.] Nachrichtenblatt des Deutschen Pflanzenschutzdienstes 32:21-24.

Ngala, B. M., P. P. J. Haydock, S. Woods, and M. A. Back. 2015. Biofumigation with *Brassica juncea*, *Raphanus sativus*, and *Eruca sativa* for the management of field populations of the potato cyst nematode *Globodera pallida*. Pest Management Science 71:759-769. Online DOI:10.1002/ps.3849

Noel, G. R., and L. M. Wax. 2003. Population dynamics of *Heterodera glycines* in conventional tillage and no-tillage soybean/corn cropping systems. Journal of Nematology 35:104-109.

Odum, E. P. 1954. Fundamentals of Ecology. Philadelphia, PA, USA: W. B. Saunders Company.

Roessner, J. 1987. Pilze als Antagonisten von *Globodera rostochiensis*. Nematologica 33:106-118.

Scholte, K. 2000. Screening of non-tuber bearing Solanaceae for resistance and induction of juvenile hatch of potato cyst nematodes and their potential for trap cropping. Annals of Applied Biology 136:239-246.

Schouten, H. J., and J. E. Beniers. 1997. Durability of resistance to *Globodera pallida* I. Changes in pathogenicity, virulence, and aggressiveness during reproduction on partially resistant potato cultivars. Phytopathology 87:862-867.

Scurrah, M. I., B. Niere, and J. Bridge. 2005. Nematode parasites of *Solanum* and sweet potatoes. Pp. 193-220 *in* M. Luc, R.A. Sikora, J. Bridge (eds.). Plant parasitic nematodes in subtropical and tropical agriculture. Wallingford, UK: CAB International.

Stirling, G. R. 1991. Biological control of plant-parasitic nematodes: Progress problems and prospects. Wallingford, UK: CAB International.

Thielemann, R. and W. Steudel. 1973. Nine years experience with monocultures of sugar beet in soil infested with *Heterodera schachtii* (Schmidt). Nachrichtenblatt des Deutschen Pflanzenschutzdienstes 25:145-149.

Thomason, I. J., and D. Fife. 1962. The effect of temperature on development and survival of *Heterodera schachtii* Schm. Nematologica 7:139-145.

Tiilikkala, K. 1991. Effect of crop rotation on *Globodera rostochiensis* and on potato yield. EPPO Bull. 21:41-47.

Tribe, H. T. 1977. Pathology of cyst-nematodes. Biolological Reviews 52:477-507.

Volterra, V. 1926. Variazione e fluttuazini del numero d´individui in specie animali conviventi. Memmorie dell´Accademia Nazionale dei Lincei 2:31-113.

Westphal, A. 2005. Detection and description of soils with specific nematode suppressiveness. Journal of Nematology 37:121-130.

Westphal, A., and J. O. Becker. 1999. Biological suppression and natural population decline of *Heterodera schachtii* in a California field. Phytopathology 89:434-440.

Westphal, A., and L. J. Xing. 2011. Soil suppressiveness against the disease complex of the soybean cyst nematode and sudden death syndrome of soybean. Phytopathology 101:878-886.

Woods, S. R., P. P. J. Haydock, and C. Edmunds. 1999. Mode of action of fosthiazate used for the control of the potato cyst nematode *Globodera pallida*. Annals of Applied Biology 135:409-415.

Xing, L. J., and A. Westphal. 2006. Transferring soil suppressiveness against *Heterodera glycines* under field conditions. Journal of Nematology 38:302 (abstract).

Zawislak, K., J. Tyburski, and B. Rychik. 1989. Significance of crop rotation and cultivars resistant to potato cyst nematode on potato production. Pp. 111-119 *in* J. Vos, C. D. Van Loon, and G. J. Bollen (eds.). Effects of crop rotation on potato production in the temperate zones. The Netherlands: Springer.