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SLU Risk Assessment of Plant Pests

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Options to manage populations of *Globodera pallida* and *G. rostochiensis*

- questions related to crop rotation, resistance of potato and pathotypes

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Background and questions

The potato cyst nematodes *Globodera pallida* [EPPO code: HETDPA] and *Globodera rostochiensis* [EPPO code: HETDRO] are regulated in the EU as union quarantine pests and listed as known to occur in the union territory ((EU) 2019/2072). A new commission implementing regulation sets out the requirements and measures established to eradicate and prevent the spread of *G. pallida* and *G. rostochiensis* in the EU ((EU) 2022/1192). In terms of eradication, specific requirements and measures are imposed on infested production sites depending on their intended use. In the case of infected productions sites used for producing potato tubers *not* intended for planting, the sites shall be subject to an official control programme to prevent further spread of the nematodes ((EU) 2022/1192, Article 8, Point 2). Each Member State can develop their own official control programme but shall, as applicable, take into account a set of elements. One of the listed elements refer to "other agronomic options for pest suppression, as mentioned in point 1 of Annex III to Directive 2009/128/EC", which in turn contains a list of management options such as crop rotation, use of adequate cultivation techniques (e.g. stale seedbed technique and sowing dates) and use, where appropriate, of resistant/tolerant cultivars.

According to the EU regulation, official re-sampling to revoke the requirement of measures can be done after a minimum period of six years counting from the last potato crop (or last detection of the pest). This period may be reduced to three years if effective (and officially approved) measures have been implemented.

In the context of the general management options listed in Directive 2009/128/EC, the following specific questions were raised by the Swedish Board of Agriculture in relation to potato cyst nematodes:

> **Q1:** How many years without growing potato is required to reduce the nematode population levels significantly?
>
> **Q2:** Are there any other crops that can increase the efficiency of the crop rotation?
>
> **Q3:** Is there any data showing how efficient the option of a trap crop is?
>
> **Q4:** How short should the cultivation cycle for potatoes be, to achieve suppression of the nematode population and to prevent development of vital cysts?
>
> **Q5:** What strategy should be used when selecting resistant cultivars in the crop rotation in order to decrease the likelihood of developing resistance-breaking populations?
>
> **Q6:** Several sources state that if a potato cultivar is resistant against the *G. rostochiensis* pathotype Ro1 it is also resistant against pathotype Ro4. Can this be used in the recommendations for selection of potato cultivars in the Swedish control programme?

Q7: Can it be assumed that a potato cultivar resistant against Ro2 and Ro3 is also resistant to some degree against Ro5, or is specific testing required to decide whether a potato cultivar is resistant against Ro5?

Q8: According to EPPO PM 9/26 the *G. pallida* pathotype Pa1 is only found on the British Isles in the EPPO region. Is this still correct?

The SLU Risk Assessment of Plant Pests was requested by the Swedish Board of Agriculture to review and analyse the scientific evidence available and provide a summary of the current knowledge in relation to these questions. The report aim to contribute with information relevant for the development of an official control programme of potato cyst nematodes in Sweden.

Crop rotation as a strategy to reduce potato cyst nematode populations

Crop rotation is frequently used to reduce potato cyst nematode populations. The following key aspects of the life cycle of the potato cyst nematodes are relevant for understanding the influence of crop rotation and crop selection on the potato cyst nematodes:

- Hundreds of eggs can be produced by each female potato cyst nematode. – As a consequence, more than a 100-fold increase in the number of nematodes during one season have been recorded (Dandurand and Knudsen 2016) and from low initial populations a 30-40 fold increase is normally the case for *Globodera rostochiensis* (Andersson 2018).

- The hatching of eggs is triggered by host root diffusates, meaning that particular chemical signals are released by plants of the Solanaceae family. As a consequence, the use of resistant host plants in the crop rotation is much more efficient than non-host crops. This is because resistant host plants are not only unsuitable for reproduction but also actively cause mortality by triggering the hatching of eggs that otherwise could have survived for decades awaiting the arrival of a host.

- Soon after hatching, the juvenile locates and enters its host plant. Within the host, the nematodes develop to vermiform males and spherical females. The male nematodes then leave the root whereas the females remain inside the host. The females deposit eggs within their own bodies and when they die their bodies harden and form a protective covering known as a "cyst". The cysts separate from the roots and has the potential to persist in the soil for decades. – As a consequence, it may take decades before all potato cysts nematodes are gone from a field if management only depends on a crop rotation which do not include plants from the Solanaceae family (Turner 1996; Holgado et al. 2015).

A review of the current knowledge in relation to the specific questions raised by the Swedish Board of Agriculture will here follow.

Q1: How many years without growing potato is required to reduce the nematode population levels significantly?

Growing plants that do not belong to the Solanaceae family, will reduce the population levels of potato cyst nematodes. This is because, also without the root diffusate trigger, a certain proportion of the eggs will hatch spontaneously when the soil temperature and moisture content are suitable (Turner and Evans 1988). A common recommendation is to have 6-7 years without potatoes to reach population levels below the damage and detection thresholds (for both *G. rostochiensis* and *G. pallida*) (EPPO 2023a, b).

The rate of decline of potato cyst nematodes recorded when a non-host is grown in a field varies substantially between individual studies. A decline rate of 35% per year is commonly assumed. This figure is based on data from a large number of small-scale studies (Been et al. 2019). A similar decline rate is commonly employed in European statutory schemes (33% per year) (EFSA et al. 2012). These general decline rates do however provide a poor estimate of the decline rate under the climatic conditions occurring in Sweden. A study based on field data from 19 sites distributed across different parts of Sweden showed that the population decline of *G. rostochiensis* was remarkably high the first year after susceptible potatoes were grown (Andersson 1987). It also showed that the rate of decline during the first year differed markedly between regions, i.e. it was in the order of 80-90% in the northern and middle parts of Sweden but approximately 60% in southern Sweden. Further, the population decline was much slower the following years, i.e. the decrease in the second, third and fourth year after susceptible potatoes were grown was 40-60% per year in northern Sweden and 20-30% in southern Sweden (Andersson 1987).

A recent large-scale study in the Netherlands show a similar pattern for *G. pallida* with a much faster decline during the first year after a potato crop than during later years (Been et al. 2019). The study also shows that soil type influences the rate of decrease. In sandy and peaty soils the decline was faster than in marine clay and loamy soils. Further, they found that the decline of *G. pallida* was faster than that of *G. rostochiensis.* However, other studies show the opposite pattern, i.e. that the decline of *G. pallida* was slower than that of *G. rostochiensis* (Sasaki-Crawley (2012) citing other articles).

Based on the values from Sweden, the required crop rotation length for a stable system would be nine years in southern Sweden and four years further north (Andersson 1987). This calculation is based on the assumptions that no other management measures are applied and a 30-fold increase in nematode numbers when a susceptible potato cultivar is planted in soil with very low densities of *G. rostochiensis*, i.e. 1.5-3 eggs per gram soil (which is the level when damage starts occurring). From an applied perspective, it is however important to know that there were also large variations between sites within regions. Thus, it is difficult to predict the decline in an individual field.

Q2-4: Plants that can be used to increase the effect of crop rotation

The approach to use crop rotation is appealing for a pest with such a narrow host range as potato cyst nematodes, the only other susceptible host that is cultivated in open field in Sweden is tomato (and that is mainly hobby cultivation) (Andersson 2018). However, classical crop rotation with non-host crops is not as efficient in the management of potato cyst nematodes as it is in many other systems. The reasons for this, as mentioned earlier, are the requirement of root diffusates from solanaceous plants for the triggering of egg hatching (Perry 1989) and that unhatched eggs can persist in the soil for decades (Turner 1996). Consequently, the effect of a crop rotation without other solanaceous plants relies solely on the spontaneous hatching of eggs. The occurrence of weeds such as *Solanum nigrum* (sv. nattskatta) may hamper the impact of such a crop rotation further.

To increase the effect of crop rotation a trap crop may be used, i.e. a crop that releases root diffusates that trigger hatching of the eggs but where the completion of potato cyst nematode life cycle is prevented in one or another way. Growing non-host plants from the Solanaceae family fall within this category as well as cultivation of potato for early harvesting. The following sections aim to answer the following specific questions; (Q2) Are there any other crops that can increase the efficiency of the crop rotation?, (Q3) Is there any data showing how efficient the option of a trap crop is? and (Q4) How short should the cultivation cycle for potatoes be, to achieve suppression of the population and to prevent the development of vital cysts?

Using non-host plants from the Solanaceae family

Solanum sisymbriifolium

The utilization of *Solanum sisymbriifolium*, also known as sticky nightshade (sv. blek taggborre), as a trap crop has relatively recently emerged as a commercially accessible method to reduce potato cyst nematode populations. In addition to the trap crop effect it appears that eggs exposed to root exudates of *S. sisymbriifolium*, which contains steroidal glycoalkaloids, may reduce the nematodes ability to complete its development on subsequent potato crops (Dandurand et al. 2019; Sivasankara Pillai & Dandurand 2021). An advantage of using *S. sisymbriifolium*, compared to using resistant potato cultivars, is that no species or pathotypes of potato cyst nematodes can reproduce in it (Dandurand & Knudsen 2016; Dias et al. 2017; Dandurand et al. 2019a). In Sweden, few growers know which pathotype, or pathotypes, they have in their fields,[1] which is problematic in terms of using resistant potato cultivars since the level of resistance against different pathotypes generally differs. According to Mhatre et al. (2022), there are currently no registered cultivars possessing complete resistance to both *G. rostochiensis* and *G. pallida*, including all pathotypes. Thus, *S. sisymbriifolium* can be used without knowledge about the virulence of the nematode population present in a field and may be especially valuable if resistant breaking pathotypes are present.

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[1] Pers. comm., I. Areskoug, Swedish Board of Agriculture

Another advantage of using *S. sisymbriifolium* instead of early potato as a trap crop is that no tubers are produced and thus no volunteer plants the succeeding year. Further, it can be ploughed down as green manure (Timmermans, 2005; Harper Adams University 2015) and due to that the roots penetrates deeper than fumigants it is efficient at deeper depths (Scholte & Vos 2000; Timmermans et al. 2006). Previous studies of the efficiency of *S. sisymbriifolium* as a trap crop has found that a reduction of the nematode population of more than 99% can be achieved compared with a control treatment (fallow) (Dandurand et al. 2019a; Chhetri et al. 2023). Cultivation of *S. sisymbriifolium* as a trap crop is most efficient when done at least two years after a potato crop. In extensive field trials in the Netherlands the population decline varied between 15% and 72% with an average of 52% (the comparable decline for fallow and resistant potato was 23% and 80%, respectively) (Hartsema et al. 2005). They concluded that planting of *S. sisymbriifolium* should not be done the first year after a potato crop since e.g. the level of triggered hatching due to the level of root diffusates from the potato crop is already high the first year. Further, black fallow is preferable the first year after a potato crop since it is very difficult to remove volunteer potato plant among other crops. Scholte and Vos (2000) found that the effect of planting *S. sisymbriifolium* the first year after growing potato was less than planting it the second year and they suggested that this may be due to that a proportion of the 1-year-old population may be in diapause. That the effect is limited of planting *S. sisymbriifolium* the first year after growing potato is also indicated in a study from Portugal (Dias et al. 2017). In addition, it is difficult to manage volunteer potatoes stemming from the previous potato crop in fields grown with *S. sisymbriifolium* (Hartsema et al. 2005).

A field experiment in northern Poland showed that the climatic conditions in Poland were suitable for growing *S. sisymbriifolium* and that it was an effective trap crop for *G. rostochiensis* (Malinowska et al. 2015). They found that the planting density of *S. sisymbriifolium* had some influence of the effectiveness, where one plant per m^2 caused a population reduction of 61% whereas the maximum population reduction was achieved with 25 plants per m^2, which reduced the population with 78%.

Importantly, all work that has only assessed the population decline as the number of eggs have underestimated the total effect of planting *S. sisymbriifolium*. Recent work shows that in addition to triggering egg hatching and thereby decreasing the number of eggs remaining in the soil, *S. sisymbriifolium* also influences the reproduction capacity of the nematodes. In one greenhouse study no difference in number of eggs after growing *S. sisymbriifolium* for 16 weeks compared to fallow was found, however, the offspring in the potato crop grown in the succeeding year was only 0.1% of the initial population (Dandurand & Knudsen 2016). Similarly, Dandurand et al. (2019a) not only found a reduction of the number of eggs by 23-50% but also a 99-100% decreased reproduction of *G. pallida* on the succeeding potato crop compared with the fallow treatment. Finally, in agreement with previous results, Chhetri et al. (2023) found in their study that the reproduction was reduced by up to 99%. The decrease in reproduction the following year may be due to chemical defence compounds, such as steroidal glycoalkaloids, present in *S. sisymbriifolium*, which has a deleterious effect on reproduction (Sivasankara Pillai & Dandurand 2021). In conclusion, these recent results are a “game changer” and can explain why practical use of *S. sisymbriifolium* as a trap crop has been deemed effective despite that some experiments have not shown a dramatic reduction in the number of eggs.

Solanum sisymbriifolium is mentioned as a trap crop in EPPO's official suppression measures to be taken to suppress populations of *G. pallida* and *G. rostochiensis* in infested fields (EPPO 2018). Further, it is commercially sold both in Europe and in North America as a trap crop for potato cyst nematodes (Sparkes 2013; AHDB 2018). However, the climatic conditions influence whether it can be used in a certain region and early work based on a crop growth model showed that Sweden falls within a zone where there is potential for sufficient growth if *S. sisymbriifolium* is allowed to grow throughout the entire growing season (Timmermans et al. 2009). However, except in the most southern part of Sweden, the minimum crop biomass was not reached in all four modelled years and the authors therefore state that "…one might conclude too much risk of failure would be associated with the use of *S. sisymbriifolium* as a control method in Scandinavia". Currently, however, there is also empirical evidence from several countries. Field data from Norway show that successful establishment of *S. sisymbriifolium* could be achieved in Scandinavian conditions by ensuring proper weed management and selecting the appropriate sowing time (Holgado and Magnusson 2010; 2012, Holgado et al. 2010; 2015). In the Netherlands, it is used at a commercial scale and is an officially recognized control measure (EFSA et al. 2012; Orlando 2022). In Scotland, they are investigating the use of *S. sisymbriifolium* with promising results, but they found it slow to establish (Orlando 2022). In Idaho, USA, they found that it had worked well as a trap crop but seeds were not always available and the farmers lost a growing season (Orlando 2022). Experience from Quebec, Canada, indicate that the *S. sisymbriifolium* does not establish well in the cool and wet soils there (Bélair et al. 2016). In conclusion, at least in the most southern part of Sweden the climatic conditions may be suitable for growing *S. sisymbriifolium.*

There are several studies that has evaluated the susceptibility of *S. sisymbriifolium* to other pests. It has for example been suggested that *S. sisymbriifolium* is susceptible to late blight (*Phytophthora infestans*) (Flier et al. 2003), but a later study showed that the susceptibility is very low (Timmermans 2005). Since oospores are produced on leaves of *S. sisymbriifolium* they can potentially add to the infection pressure on potato crops cultivated in the subsequent year (Flier et al. 2003; Timmermans 2005). According to a study by Scholte and Vos (2000), *S. sisymbriifolium* (accessions[2] 89-4750-017 and -018) should be considered to be highly resistant to *Meloidogyne chitwoodi* and show strong resistance against *M. hapla* (no galls developed on most of the plants) whereas in a study by Dias et al. (2012) the results indicate that *S. sisymbriifolium* cultivars Domino, Pion, Sis 4004 and Sharp are resistant to *M. chitwoodi* but hyper-susceptible to *M. hapla*. Further, an experiment by Perpétuo et al. (2021) showed that *S. sisymbriifolium* cv. Sis 6001 is resistant to *M. chitwoodi*. The *S. sisymbriifolium* accession used in the experiments by Scholte and Vos (2000) appeared to be highly resistant to *M. fallax* (Scholte and Vos (2000) citing personal communication with J. Hendrickx). Observations by Scholte and Vos (2000) indicate that *S. sisymbriifolium* is a good host for the Colorado beetle (*Leptinotarsa decemlineata*). Finally, a study has demonstrated that *S. sisymbriifolium* exhibits a relatively high degree of resistance to *Verticillium dahliae* (sv. kransmögel) (Alconero et al. 1988).

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[2] Following FAO (2023) an accession is "A distinct, uniquely identifiable sample of seeds representing a cultivar, breeding line or a population, which is maintained in storage for conservation and use."

Solanum sisymbriifolium is also considered as an invasive species in some areas. The plant species originates from South America and is available in the horticultural trade for its aesthetic value and edible fruit (EPPO 2023c). It is on the EPPO alert list of invasive species since it has established in Sardinia (IT) where it is considered a threat to irrigated crops and native wild plant species due to its capacity to compete with other plants. It is also considered to be a danger to livestock and humans due to its sharp spines. When it has established, it often forms dense spiny thickets and outcompete the native vegetation and it is considered a noxious invasive weed in Australia, South Africa, USA, Cuba, Hungary, Italy, Spain, China and Japan (Rojas-Sandoval 2023). *Solanum sisymbriifolium* has become naturalized in 17 states in USA (USDA 2023a) but is not listed as noxious or invasive in any of them (USDA 2023b). However, a weed risk assessment concluded that the plant constitutes a high risk due to its spread capacity and impacts in especially pastureland (USDA 2013). In the Netherlands, the risk that *S. sisymbriifolium* would become a weed was assessed to be small, e.g. since the initial growth in the spring is very slow and thus its competitive strength would be poor (Timmermans 2005).

In Sweden, *Solanum sisymbriifolium* occurs in open habitats such as fields, farms and wasteland but is considered a very rare species (Mossberg & Stenberg 2003). Accordingly, only 65 records from Sweden are available in GBIF (2023) and it has only been found in the southern and middle parts. It was observed in Sweden already in 1927 (Herloff 2011). It is classified as "Ephemeral (including long-persisting relics of cultivation)" in Sweden (Karlsson 1998). Observation by Scholte (2000b) suggest that the plants cannot survive winter frost.

The likelihood of natural spread is decreased by the commercial practice to top *Solanum sisymbriifolium* before berries fully form (a procedure that also have the advantage that it encourages regrowth and thereby the efficiency of the trap crop (Sasaki-Crawley 2012; Dias et al. 2017; Scholte 2000b).

Solanum nigrum and *S. scabrum*

Solanum nigrum (sv. nattskatta) is a common weed in Sweden (Andersson 2018). It has however also been suggested as a trap crop for potato cyst nematodes, but it was not as effective as *S. sisymbriifolium* in reducing potato cyst nematode populations in the soil (Scholte 2000c; Scholte & Vos 2000). An unpublished pot experiment showed a decrease in potato cyst nematode eggs with 45-76% where the level of control was influenced by year, soil type and origin of seeds (AHDB 2018). In another unpublished pot experiment in the UK, the reduction of eggs was even higher, between 80-91% (Sparkes 2013). There are 'varieties' of *S. nigrum* that are completely resistant to *G. rostochiensis* and have a high level of resistance to *G. pallida* (Scholte 2000c). However, it should be noted that the nematodes can multiply on some varieties, but it appears to depend on the geographical source of the plant material (Van Riel and Mulder 1998; Sparkes 2013; Fatemy and Ahmarimoghadam 2019). If used as a trap crop it is necessary to prevent them from becoming weeds. However, experiments showed that cutting the crop at flowering time was of limited value for preventing seed production since berries are produced on the plants very close to the soil surface (Scholte 2000b).

Solanum scabrum (sv. bärskatta) is considered "Ephemeral (including long-persisting relics of cultivation)" in Sweden (Karlsson 1998). *Solanum scabrum* have been shown to grow well under Dutch conditions and it strongly induced hatching but did not show complete resistance

(Scholte 2000c). In Kenya, potato cyst nematode densities decreased by more than 80% after three successive seasons of cultivations of *S. scabrum* (Chitambo et al. 2019). The potato cyst nematodes were treated as a group but both *Globodera rostochiensis* and *G. pallida* were found in the field. The authors recommend the use of *S. scabrum* since it simultaneously controls potato cyst nematodes and root knot nematodes (*Meloidogyne* spp.). *Meloidogyne hapla* was reported to occur in the studied field while neither *M. chitwoodi* nor *M. fallax* were detected.

Cultivation of potato for early harvesting

Growing potato (*Solanum tuberosum*) for early harvest as a trap crop to reduce the populations of potato cyst nematodes has a very long history and with a vast number of studies conducted reporting results of this approach. The approach is not dependent on the use of resistant cultivars since it simply builds on planting and growing the potato as long as possible, to maximize nematode infection, but harvest before the start of nematode reproduction (Holgado and Magnusson 2010). Here, we only provide an overview of the effectiveness of this approach, and the factors that influence the effectiveness, focusing on Swedish conditions.

Reviewing some earlier studies, Scholte (2000a) state that between 40% to over 90% reductions in populations have been achieved using susceptible potato as a trap crop. Thus, there is no doubt that this approach can be very efficient and consequently it is practised in many countries, e.g in Sweden (Andersson 2018), Finland (Finnish Food Authority (Ruokavirasto) 2022), Norway (Holgado and Magnusson 2010), Belgium (Ebrahimi et al. 2014), and the Netherlands (Orlando 2022). In the Netherlands, they are using a specific variant of early harvesting as an emergency method to control potato cyst nematodes (Orlando 2022; Orlando and Boa 2023). The potato is planted at double the typical density and after 40 days, glyphosate is applied to the canopy. Within 24 to 48 hours, the roots die, effectively halting the growth of nematodes. By using a herbicide some of the e.g. practical challenges with harvesting at an exact date are reduced. It is an official and recognized control option, but it is only used in extreme circumstances since it takes a lot of effort and resources.

The length of time over which the potato is grown has major consequences on its effect. More nematodes will be trapped the longer the potato crop is allowed to grow since that allows a higher percentage of the juveniles to invade the roots. However, when susceptible potatoes are allowed to grow too long the nematode population will increase instead of decrease. A fixed date for harvesting is often used for the strategy of growing potatoes for early harvesting as a trap crop. Since the temperature requirement for potato cyst nematodes vary between different regions, with lower requirements further north (Ebrahimi et al. 2014), different dates for harvesting have been used in different countries. Some examples are;

- In Sweden, historically, it was believed that harvesting the potato before Midsummer, which falls between June 20th and June 26th, could effectively control the populations of potato cyst nematodes, even when potatoes were grown annually (Andersson 2018). However, due to earlier and earlier planting practices and the use of plastic sheets during planting, it has been suggested that this assumption is unlikely to hold true (Andersson 2018).

- In Finland, the use of potato as a trap crop is allowed if it is harvested and the plants destroyed at the latest the 7th of July[3] according to the Finnish official program for control of potato cyst nematodes (Finnish Food Authority (Ruokavirasto) 2022).

- In Belgium, the corresponding date is 20th of June (Ebrahimi et al. (2014) citing another source). However, field data show that this date is too late, since both *Globodera rostochiensis* and *G. pallida* formed cysts earlier than that date (Ebrahimi et al. 2014).

Since a fixed harvesting date does not take into account the influence of when the potato crop is planted, another measure is sometimes used, which is days after planting. According to Tiilikkala (1987), harvesting of fields infested with *G. rostochiensis* must occur 70-75 days after planting in the climatic conditions prevailing in Finland. According to Holgado et al. (2015), the corresponding figure is 40 days for Norway and according to Hansen & Jacobsen (1985) the corresponding figure is 85-90 days for Denmark. The population growth of *G. pallida* is a bit faster and it has been suggested that fields infested with this species should be harvested about seven days earlier (Webley & Jones 1981). An example of the effect that can be obtained with a fixed planting date and a fixed growth period is provided by an eight-year long study in UK where potato was planted the 11th of March each year and harvested 83 days later (Webley & Jones 1981). In every year except one, which was exceptionally warm, the decline of the nematode population was on average 55%.

Since the temperature varies between years, the decision of when to harvest can be assumed to be considerably improved if the harvest date instead would be based on number of degree-days. Degree-days is the accumulated daily difference between the mean temperature and base temperature. The base temperature being the lowest temperature when development occurs. Based on a study in growth cabinets simulating Nordic conditions it was concluded that good results should be obtained in fields infested with *G. rostochiensis* if early potato is harvested before 400-500 degree-days have accumulated (with 6 °C as the base temperature) since the potato was planted (Magnusson 1986). Note that this study was conducted using only one nematode population of *G. rostochiensis* from Uppsala. Since populations of *G. rostochiensis* or *G. pallida* can differ in the number of degree days required, more accurate values may be obtained by studying additional regional nematode populations. Based on field data, Tiilikkala (1987) suggested that early potato should be harvested in Finland before 700 degree-days (with 4.4 °C as the base temperature). Based on results from field and laboratory experiments, Hansen & Jacobsen (1985) suggested that the corresponding figure for Denmark is 440 degree-days (with 6 °C as the base temperature).

Some disadvantages with using susceptible potato as a trap crop mentioned in the literature are the following:

- It is considered to be a risky strategy due to the unpredictability of the weather, that is, one season may be uncommonly warm or it may be too wet to harvest at the right time

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[3] In addition, it is required that a cover crop must be sown in the field no later than two weeks after the entire potato crop in the field in question has been harvested.

(Holgado et al. 2015; AHDB 2018). Further, other factors than temperature influence the development time of the nematodes.

- Tubers that remain in the soil after harvesting, as little as one volunteer potato plant per m^2 the following year can result in an increase of the potato cyst nematode population (Van Riel and Mulder 1998).

- The use of potato as a trap crop has been shown to increase infestations with *Meloidogyne hapla* (however it may decrease stem infections by *Verticillium dahliae* in the succeeding crop, probably due to that potato cyst nematodes stimulate stem infections by *V. dahliae* and the trap crop decrease the population levels of potato cyst nematodes) (Scholte 2000a).

- Consistent early planting of potato appears to select for fast developing nematode populations (Hominick 1982; Magnusson (1986) citing other sources).

Conclusions

Using a trap crop such as *S. sisymbriifolium* can significantly reduce potato cyst nematode populations, especially when grown at least two years after growing potato. In Sweden, it is likely that a full season would be required to achieve sufficient root development. Experiences from some countries emphasize the challenges of growing it, e.g. due to competition from weeds and climatic constraints. *Solanum sisymbriifolium* has been present in Sweden at least since 1927 without any reported problems. However, it is currently a rare species and before growing it at a large scale, potential risks should be considered, especially since this species is regarded as invasive in some countries. Further, it should be noted that *P. infestans* (which cause late blight of potato) can produce oospores on *S. sisymbriifolium*. *Solanum nigrum* and *S. scabrum* are alternative trap crops but they have not been investigated to the same extent as *S. sisymbriifolium.*

Using potato for early harvest as a trap crop can effectively reduce potato cyst nematode populations but the cultivation length is essential for the outcome. Due to the annual variability of the weather, it is recommended that timing of harvest is related to the number of degree days obtained during the season. Previous studies in Sweden suggest that harvesting before 400-500 degree days (base 6°C) could be used, but this should be further verified to account for the potential variability of nematode populations across the country.

Nematode pathotypes and resistant potato cultivars

Several pathotypes have been described for both *G. rostochiensis* and *G. pallida*. Kort et al. (1977) described five different pathotypes in Europe for *G. rostochiensis,* Ro1 - Ro5, and three different pathotypes for *G. pallida*, Pa1 - Pa3. In this pathotype scheme, a set of differential *Solanum* clones were used to differentiate between nematode populations based on their capacity to reproduce on the different clones. A "differential *Solanum* clone" refers to a specific *Solanum* genotype that is used as a standard for comparison in disease resistance testing and research. This scheme has been used to describe the distribution of the different pathotypes in Europe and as a basis for management. However, following its publication, a number of issues related to the pathotype scheme by Kort et al. (1977) were raised. In short, the scheme was not considered to provide adequate results due to reasons related to (i) the differential *Solanum* clones included and the resistance they represent, (ii) the diversity of virulence genes present within the nematode populations tested and (iii) the method used to assess the reproductive rate on the clones (Trudgill 1985; Mugniéry et al. 1989; Nijboer and Parlevliet 1990).

Some of the *Solanum* clones used in the scheme represent resistance derived from major genes providing qualitative resistance (e.g. H1 and H2) (Mugniéry et al. 1989; Strachan et al. 2019). Qualitative resistance is the result of one or few major genes providing a resistance that is distinct, the plant is either resistant or susceptible (D'Arcy et al. 2001). Thus, individual nematodes either can or cannot multiply on these clones depending on the respective virulence gene they carry. Pathotypes Ro1 or Ro4 cannot reproduce on cultivars with H1 resistance while all other pathotypes of *G. rostochiensis* can. Similarly, Pa1 is unable to reproduce on cultivars with H2 resistance while Pa2 and Pa3 can. Therefore, if the nematode population being tested is homogenous this will enable a classification into these pathotypes (Ro1/Ro4 or Pa1) or not (Mugniéry et al. 1989). If the nematode population is heterogenous, composed of individuals both with and without the virulence genes breaking the resistance of H1 and H2, the results will not be so clear. Some of the other differential *Solanum* clones included in the scheme by Kort et al. (1977), displayed resistance due to several resistance sources providing quantitative resistance and partial resistance (Mugniéry et al. 1989). Quantitative resistance is the result of several genes (for example represented by different QTLs[4]), providing a resistance that can not be divided into distinct categories, instead the resistance vary continuously from resistant to susceptible (Pilet-Nayel et al. 2017; D'Arcy et al. 2001). Often only partial resistance is obtained in the plant meaning that e.g. pathogen multiplication or disease are reduced but not totally prevented (Pilet-Nayel et al. 2017). Multiplication of individual nematodes on these clones will be due to a combination of virulence genes they carry which could result in a range of different reproductive rates. This in combination with the fact that many of the nematode populations are heterogeneous with regard to both species and virulence groups complicates the interpretation of the test.

The nematode populations (of both species) often appear to consist of individuals that differ in virulence, i.e., different frequencies of the virulence genes occur in different populations (Trudgill 1985). This means that different proportions of specific virulence will result in certain

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[4] A Quantitative Trait Locus (QTL) is a region of the DNA associated with a specific phenotypic trait.

population build up on the differential clones but does not represent a distinct pathotype (Trudgill 1985). The separation of pathotypes based on the differential clones displaying partial resistance was also found to be inconsistent due to the measure used to separate the pathotypes (Trudgill 1985). Kort et al. (1977) used a separation of susceptible and resistant clones based on a reproductive rate (Pf/Pi)[5] as being larger or smaller than one, respectively, without relating it to a non-resistant control. Different environmental factors, such as initial population density of the nematodes and test procedure thus had an impact on the resulting reproductive rate obtained leading to low reproducibility (Trudgill 1985). Such effects are especially observed in hosts being partially resistant or not resistant (Mugniéry et al. 1989). Thus, although there are different pathotypes (virulence) present they cannot be distinguished reliably because of the mixed presence in populations and the polygenic resistance (i.e. resistance provided by several genes) found in some of the *Solanum* differentials. Generally, it is considered that only pathotypes Ro1 (including Ro4) and Pa1 can clearly be separated from other populations of respective species and that the other pathotypes described by Kort et al. (1977) consists of populations with overlapping virulence (EPPO 1985; EPPO 2023b).

Because of these limitations of the pathotype scheme, its use is not recommended (cf. EPPO 2018; EPPO 2022). But no alternative scheme is available describing the procedure to separate pathotypes of potato cyst nematodes reliably. Nevertheless, pathotype testing is still being performed in e.g. Sweden (Rölin 2023). Further, the pathotypes classified according to Kort et al. (1977) are still frequently referred to both in the current legislation ((EU) 2022/1192) as well as in current standards for risk management (EPPO 2018, 2021). For example, resistance testing of new potato cultivars shall include a standard set of nematode populations referring to different pathotypes, i.e., Ro1 - population Ecosse, Ro5 - population Harmerz, Pa1 - population Scottish, Pa3 – population Chavornay[6] (following the EPPO standard PM3/6(2) (EPPO 2021) and (EU) 2022/1192). In addition, there are recommendations that the pathotype of local nematode populations should be described both in relation to tests determining the resistance of new potato cultivars and in relation to risk management strategies, e.g., in order to select potato cultivars with appropriate resistance or to describe new resistance breaking populations (EPPO 2018; (EU) 2022/1192; EPPO 2021).

EPPO standard PM3/6(2) describes the procedure to assess the degree of resistance of potato cultivars to the potato cyst nematodes (EPPO 2021). According to this, a standard set of nematode populations are used (see above), and the degree of resistance is classified according to the relative susceptibility compared to a standard susceptible control cultivar ($Pf_{test\ cultivar}/Pf_{control\ cultivar} \times 100$). The degree of resistance is divided into nine classes designated by a score 1-9. Score 1-3 represent susceptible cultivars with a relative susceptibility of >100 - >25%, scores 4-7 represents partially resistant cultivars with a relative susceptibility ranging from of ≤ 25% to > 3% while scores 8-9 represents resistant cultivars with relative susceptibility of ≤ 3% (EPPO 2021; Gartner et al. 2021). Following the EU regulation (2022/1192), the highest levels of resistance, i.e., a score of 8-9, where available, should be used as part of

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[5] Pi = initial nematode population density, Pf = population density at harvest

[6] Referred to as pathotype Pa2/3 by Ruthes and Dahlin (2022).

official control programmes. Information about the assessed level of resistance for different potato cultivars provided by different countries is listed in Appendix 1.

To conclude, the pathotype classification used to describe the virulence of nematode populations is useful for practical applications, but it is important to be aware of the limitations in terms of its capacity to differentiate between ‘true’ pathotypes.

Q5: What strategy should be used when selecting resistant cultivars in the crop rotation in order to decrease the likelihood of developing resistance-breaking populations?

Development of resistance-breaking potato cyst nematode populations

Intensive use of potato cultivars that carry resistance against certain virulence can lead to selection of *Globodera* species and in altered virulence patterns within single-species populations. Intensive use of cultivars resistant against *G. rostochiensis* (carrying H1 resistance) has for example led to an increased frequency of *G. pallida* (which is virulent against such potato cultivars) in for example the UK, Portugal and Switzerland (Minnis et al. 2002; Camacho et al. 2020; Ruthes and Dahlin 2022; Orlando 2022). Furthermore, in Germany and the Netherlands, a new virulence type was discovered in 2014/2015 when populations of *G. pallida* were found to multiply on potato cultivars carrying resistance against Pa2/3[7] (Niere et al. 2014; Mwangi et al. 2019; Grenier et al. 2020). This population in Germany is referred to as the Oberlangen populations but the pathotype has not been established (Mwangi et al. 2019; EPPO 2021). These virulent populations belong to the European gene pool and appear to have adapted to the resistant potato cultivars used (Grenier et al. 2020). Grenier et al. (2020) also reported preliminary results that suggest that this resistance breaking was due to a single adaptation event. In the region in Germany, where this virulent population was first reported, starch potatoes have been grown every two years (Grenier et al. 2020). There are no known potato cultivars resistant against this new virulence type (Mwangi et al. 2019).

Selection in nematode population due to differential resistance of the potato host has also been studied under laboratory conditions. Fournet et al. (2013) for example studied the durability of resistant potato cultivars in experiments with *G. pallida.* They found that the nematode population could overcome the resistance in one of the tested potato genotypes after eight generations but not in the other three tested genotypes that differed in genetic background. Moreover, the gain in virulence in the nematode population due to selection on a particular potato genotype was not observed in another potato genotype with the same resistance gene markers. Beniers et al. (2019) studied selection in a Pa2/3 population by rearing the nematodes on potato cultivars carrying different resistance genes. They found that after four generations on a cultivar which differed in resistance against Pa2 and Pa3, the relative reproductive rate increased by a factor of 61 on that particular cultivar but was also increased on other cultivars. Further, alternating rearing the nematode population between different potato cultivars had no

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[7] Pa2/Pa3 is a term that is used to characterize the broad range of virulence in European non-Pa1 populations of *G. pallida* (Bairwa et al. 2022).

effect if the resistance pattern was similar among the cultivars (in their case favouring Pa3), while alternating with a cultivar which did not select for Pa3 could delay selection. They also found that the rate of selection was mainly due to the variation of virulence levels within the nematode populations rather than the level of resistance of the potato cultivar.

Changes in virulence due to cultivation of resistant potato cultivars has also been observed in Sweden. H1 resistant potato cultivars were first introduced in the starch potato districts in southern Sweden in late 1960’s (Ireholm 1987). During the 1970’s, inventories were carried out in order to evaluate the durability of the resistance and in the late 1979 resistance breaking populations were discovered (Olsson 1981; Ireholm 1987). Studies of the genetic structure of potato cyst nematodes indicates that the Swedish potato cyst nematode populations have a considerable genetic heterogeneity, especially in populations virulent against potato cultivars carrying the H1 gene (Manduric and Andersson 2003). Further, most of the *G. rostochiensis* populations included in the study that were virulent against potato cultivars with the H1 resistance were from fields where resistant potato cultivars had been cultivated (Manduric and Andersson 2003). In Sweden, mixed populations of the two *Globodera* species are found in some fields. For example, mixed populations were found in 2.5% of in total 920 populations analysed during an inventory in 1979 (Olsson 1981). A similar proportion of 3% mixed populations were found in the annual monitoring survey performed by the Swedish Board of Agriculture in 2021 (Rölin 2023). In total, *G. pallida* and *G. rostochiensis* was found in ca 14% and ca 12% of the samples (incl. the mixed samples), respectively (Rölin 2023).

To summarize, the literature shows that the development of resistant potato cyst nematode populations as a consequence of intensive use of resistant cultivars is not only a theoretical concern but a reality. Further, the large genetic heterogeneity observed within nematode populations and the occurrence of mixed populations of the two *Globodera* species in Sweden stress the importance of adapting management measures to avoid selection of resistant potato cyst nematode populations.

Strategies to prevent the development of resistance-breaking potato cyst nematode populations

The use of resistant potato cultivars in combination with crop rotation is an important part of management programmes to control potato cyst nematodes with the purpose to suppress the nematode populations as much as possible. In terms of decreasing the likelihood of resistance breaking of the population, the approach is often not clearly stated. Nevertheless, EPPO (2018) recommend, in order to reduce the likelihood of selecting for new virulent pathotypes, to employ a minimum crop rotation of 3 years combined with efficient control of potato volunteers[8] and solanaceous weeds. Further, they state that since selection pressure may be decreased by extending the rotation to 4 years and alternating between cultivars with resistance against *G. pallida* and *G. rostochiensis*, such measures should be considered (EPPO 2018). Furthermore, ANSES (2016) recommend alternating between potato cultivars with i) different resistant genes (or at least different genetic background) and ii) resistance to both *Globodera* species, to avoid adaptation of the nematode populations and selection for one of the species.

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[8] Described in EPPO standard PM 3/089(1) (EPPO 2020)

Another suggested approach is to use resistant and susceptible potato cultivars every second time to avoid breaking resistance (Andersson 1997; 2018). If selection to more virulent nematode populations comes with a fitness cost on susceptible cultivars, as observed e.g., in experiments with *Meloidogyne incognita* infecting tomato (Castagnone-Serena et al., 2006), such an approach could decrease the likelihood of resistance breaking. However, observations from lab-experiments with potato cyst nematodes suggest that the more virulent populations created through selection, have an increased fitness and higher reproduction also on susceptible cultivars (Fournet et al., 2016; Mwangi et al., 2019). It is thus questionable how efficient an approach with alternating between resistant and susceptible potato cultivars is to decrease the likelihood of resistance breaking.

In efforts to breed for durable resistance in potato, it is frequently highlighted that this is more likely to be achieved if resistance sources are combined in the cultivars (Rouppe van der Voort et al. 2000; Jones and Varypatakis 2019; Gartner et al. 2021). Such a strategy may include; i) combining resistance to as many different pathotypes as possible, ii) combining several QTLs providing partial resistance and/or iii) combining major resistance genes with minor resistance QTLs rather than relying on monogenic resistance (Caromel and Gebhardt 2011 and references therein).

To summarize, the following strategies to prevent the development of resistant breaking potato cyst nematode populations can be recommended; i) crop rotation of at least four years (but see Q1), ii) alternating between potato cultivars with different sources of resistance or genetic background, iii) choose potato cultivars with several sources of resistance (e.g. against both *G. rostochiensis* and *G. pallida* and iv) removing all potato volunteers and other solanaceous weeds from the fields during potato free years.

In general, it can also be assumed that using a combination of management measures will decrease the selection pressure for resistant breaking pathotypes. Sampling to enable early detection of resistance breaking populations is also important for the management of such populations.

Q6: Several sources state that if a potato cultivar is resistant against the *G. rostochiensis* pathotype Ro1 it is also resistant against pathotype Ro4. Can this be used in the recommendations for selection of potato cultivars in the Swedish control programme?

Whether nematode populations classified as pathotype Ro1 and Ro4 can reproduce on a certain potato cultivar depends on the source of resistance in the selected potato cultivar. Potato cultivars with H1 resistance will prevent reproduction of both Ro1 and Ro4 (Kort et al. 1977; Gartner et al. 2021). Due to this equal behaviour on potato cultivars carrying the H1 resistance, Ro1 and Ro4 has been regarded together to represent one pathotype (e.g., EPPO 1985; Mugniéry et al., 1989; Nijboer and Parlevliet 1990). The EPPO standard for resistance testing of new potato cultivars only include a nematode population representing Ro1 and not Ro4 in the panel of standard nematode populations (EPPO 2021). Official resistance tests of potato cultivars done in Germany at the Julius Kühn Institute has not included tests of Ro4 since 2014 since it does not differ from Ro1 (Bundessortenamt 2022).

Potato cultivars carrying the H1 gene became commercially available in 1966 and H1 resistance is the most frequently used resistance in potato breeding against *G. rostochiensis* (Gartner et al. 2021). In EPPO standard PM9/26(1), a guidance is provided on the selection of resistant cultivars to match different pathotypes (EPPO 2018). Here, it is indicated that potato cultivars with resistance against either Ro1 or Ro4 can be used against both pathotypes as well as populations with mixtures of the pathotypes.

It should be noted that other QTLs have been identified to provide resistance against Ro1, but it is unclear whether they would also provide resistance against Ro4 (Caromel and Gebhardt, 2011; Gartner et al. 2021). It is also not known to what extent this resistance is included in commercial cultivars today and whether this is done without also including H1 resistance. A search in the European cultivated potato database (containing 138 cultivars assessed against both pathotypes) resulted in only one potato cultivar (Atrela) that showed different resistance level as assessed by the same institute, i.e., very low to low resistance against Ro1 but with high to very high resistance against Ro4 (ECPD, 2023). Differences in assessed resistance between Ro1 and Ro4 obtained by different institutes were found for in total four potato cultivars. The reasons for these differences are however unclear.

In conclusion, since H1 resistance appear to be included in all currently used resistant potato cultivars against Ro1, it can be assumed that these are also resistant against Ro4.

Q7: Can it be assumed that a potato cultivar resistant against Ro2 and Ro3 is also resistant to some degree against Ro5, or is specific testing required to decide whether a potato cultivar is resistant against Ro5?

In 1984 it was concluded at an EPPO Workshop on Cyst Nematodes, that Ro2, Ro3 and Ro5 are not distinct pathotypes but instead represent a continuum of virulence (EPPO 1985). However, Nijboer and Parlevliet (1990) argue that three pathotypes of *G. rostochiensis* could be reliably recognized, i.e., Ro1/4, Ro2/3 and Ro5.

In EPPO standard PM9/26(1) a guidance is provided on selection of resistant cultivars to match different pathotypes (EPPO 2018). Here it is indicated that it cannot be assumed that potato cultivars resistant against Ro2 or Ro3 also would be resistant against Ro5. Instead, if it is known that the pathotype present is Ro5 the required resistance of the potato cultivar should be specific to Ro5 according to the guidance. Likewise, a nematode population consisting of a mix of pathotypes Ro2/3/5 would require resistance against Ro5 in addition to resistance against Ro3 (incl. Ro2) or Ro2/3. It should be noted, that in the EPPO standard describing the testing of potato resistance (PM3/68(2)), the standard populations that should be used in resistance tests of new potato cultivars represents pathotypes Ro1, Ro5, Pa1 and Pa3 and that none is included yet to represent Ro2/Ro3 (EPPO 2021).

In the official resistance tests of potato cultivars done at the Julius Kühn Institute, it can be observed that both Ro2/Ro3 and Ro5 are included in the resistance tests and further that similar level of resistance is found in cultivars assessed against both Ro2/Ro3 and Ro5, but that some exceptions are found (scores 8 vs 6 for two cultivars) (Bundessortenamt 2022).

In conclusion, the literature studied do not support the assumption that potato cultivars resistant against Ro2/Ro3 automatically would be resistant against Ro5.

Q8: According to EPPO PM 9/26 the *G. pallida* pathotype Pa1 is only found on the British Isles in the EPPO region. Is this still correct?

The *G. pallida* pathotype Pa1 is known to occur in the UK and Ireland (EPPO 2018: Dandurand et al. 2019b). Nematode populations classified as Pa1 have also been reported from Tenerife, Spain (Gonzales et al. 1996; Bello et al. 2005). Øydvin (1978) state that Pa1 may occur in Norway. Further, several more recent publications also state that Pa1 occur in Norway (Magnusson and Hammaeraas 1994; Holgado and Magnusson 2010; 2014). The presence of Pa1 has been confirmed by C. Magnusson, NIBIO (pers. comm., 2023). No other reports of the presence of Pa1 in any country within Europe was found. It should however be noted that pathotype testing appear to be rarely performed in recent years. Outside of the EPPO region, Pa1 is also found in India (Bairwa et al. 2021).

The concept of pathotypes is however complex, as previously described, and the virulence types described by Kort et al. (1977) are only a small subset of those present in South American populations (Saenz and de Scurrah 1977; EFSA et al. 2012). Further, as described previously there are nematode populations with a new virulence type in Germany and the Netherlands (Niere et al. 2014; Mwangi et al. 2019; Grenier et al. 2020).

In conclusion, apart from the occurrence of Pa1 in the British Isles, the pathotype has been found in Norway and in Spain (Tenerife).

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Appendix 1. Sources of list of resistant potato varieties

Country/region	**Reference and link**	**Pathotype specific information**
Belgium	PhytoDis and others 2023 https://nematodes.be/fr/lutte/lutte-globodera/	Ro1, Ro2/3, Pa2, Pa3
European	ECPD (2023) The European cultivated potato database. European Cooperative Programme for Plant Genetic Resources (ECPGR). https://www.europotato.org/	Ro1, Ro2, Ro3, Ro4, Ro5, Pa1, Pa2, Pa3 (but unknown classification system for resistance)
Finland	Finnish Food Authority (Ruokavirasto) (2022) Peruna-ankeroisen kestäviä perunalajikkeita / Potatissorter som är resistenta mot potatiscystnematoder [Potato varieties resistant against potato cyst nematodes] https://www.ruokavirasto.fi/globalassets/viljelijat/kasvintuotanto/kasvinterveys/kasvintuhoojat/ankeroisenkestavat_lajikkeet.pdf	Ro1, Ro2/3, Ro5, Pa2, Pa3
France	Ministry of Agriculture (2019) http://45.86.205.3/docs/bsv/pommedeterre/listevarietesnematodes.pdf	Ro1/4 and Pa2/3
Germany	Federal Plant Variety Office (Bundessortenamt) (2022) Beschreibende Sortenliste Kartoffel 2022 [Descriptive List of Potato Varieties 2022]. Germany. https://www.bundessortenamt.de/bsa/media/Files/BSL/bsl_kartoffel_2022.pdf	Ro1, Ro2/3, Ro5, Pa2, Pa3
Great Britain	Agriculture and Horticulture Development Board (2023) Potato Variety Database. https://potatoes.agricrops.org/	*G. rostochiensis* (Ro1) and *G. pallida* (Pa1 and Pa2/3 together)
Switzerland	Ruthes, A.C. and Dahlin, P. (2022) The Impact of Management Strategies on the Development and Status of Potato Cyst Nematode Populations in Switzerland: An Overview from 1958 to Present. Plant Disease 2022 106:4, 1096-1104. https://doi.org/10.1094/PDIS-04-21-0800-SR (Supplementary material)	Ro1, Ro2/3, Ro4, Ro5, Pa1, Pa2, Pa3

The Netherlands	NVWA (Netherlands Food and Consumer Product Safety Authority) (2023) Lijst van in Nederland beschikbare aardappelrassen met bijbehorende resistentieniveaus voor aardappelmoeheid. [List of potato varieties available in the Netherlands with corresponding resistance levels for potato cyst nematode.] https://www.nvwa.nl/onderwerpen/aardappelmoeheid/documenten/plant/plantziekte-en-plaag/plantziekte/aardappelmoeheid/aardappelmoeheid-lijst-van-in-nederland-beschikbare-aardappelrassen-met-bijbehorende-resistentieniveaus-voor-aardappelmoeheid	Ro1, Ro2/3, Pa2, Pa3