45 Transporters of trouble: Trichodorids and Tobacco rattle virus in potatoes

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Introduction

Trichodorids may cause both direct damage to the plants as well as indirect damage through transmission of Tobacco rattle virus (TRV). Trichodorids include nematodes of among others the genera *Paratrichodorus* and *Trichodorus*, which are the most common in north-western Europe. The number of species occurring within a given region varies. Ten species are known to occur in the Netherlands and 13 species have been reported for Germany. High densities of the nematodes in spring may cause direct damage to the plants. However, indirect damage may already occur at low nematode densities when only a few nematodes are infected with TRV.

Economic importance

Trichodorids often show a patchy distribution in the field, which makes it difficult to estimate the overall effect of direct damage. When trichodorids are present in high densities (i.e. above 10 specimen/100 ml soil in the case of *Paratrichodorus teres*, above 100 specimen/100 ml in the case of other trichodorid species when based on extraction by Oostenbrink elutriation) (Actieplan Aaltjesbeheersing, 2010), yield loss can be 30–50%. Besides direct damage, even more important is the transmission of TRV by trichodorids. If potato tubers are infested by TRV, the plant tries to hinder further spread of the virus by a hypersensitive response. As a result of this defence response, local lesions, ringspots or line patterns of corky tissue are formed in the tuber. The disease is called ‘spraing’ or corky ringspot (Fig. 45.1).

Because of this qualitative damage, potatoes are worthless for the processing industry and unattractive as ware potatoes. For seed potatoes, the Dutch inspection service (Nederlandse Algemene Keuringsdienst) allows a maximum of 6% infested tubers (NAK, 2020). Higher levels will result in rejection of the entire containment. The official threshold for ware potatoes is similar, but companies usually set their own threshold at a much lower level. Whereas some companies require ware potatoes to be absolutely free of symptoms, other companies do allow some damage up to 2%. Those requirements may also depend on the amount and quality of the potatoes that are available. With respect to seed potatoes, some countries even require PCR testing for import, with zero tolerance for the occurrence of TRV. This poses the risk that lots visually free from symptoms are rejected because of latent virus infection.

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Fig. 45.1. Symptoms of spraing in potato tubers caused by infection with TRV transmitted by trichodorid nematodes. Photograph courtesy of Wageningen University & Research, Field Crops.

Host range

The host range of trichodorid nematodes is broad, and the host status of many crop species is still unknown. Plants that are known to multiply at least some of the most common trichodorid species are potato, sugar beet, onion, carrot, maize, *Phaseolus* beans, cabbage, wheat, barley, rye and ryegrasses (Best4Soil, 2020), as well as strawberries and a range of tree and fruit tree species. Also, many wild plants that occur as arable weeds are able to multiply trichodorids.

Distribution

In a sampling of 500 arable fields throughout the Netherlands, trichodorids were found in 60–70% of the samples from sandy soils in the eastern part of the country (Keidel *et al.*, 2007). In a large-scale sampling of grasslands in the Netherlands, trichodorids were found in about 40% of the samples from sandy soils (de Boer *et al.*, 2019). When soil conditions are known to be favourable for a nematode species, the area that theoretically is sensitive to damage may be estimated. Based on a description of the texture and organic matter and lime content of the topsoil, and the texture of deeper layers in the soil profile, it was estimated that 18–27% of the soils in the Dutch marine clay area may be sensitive to direct damage by *P. teres* (de Smet and van Soesbergen, 1968). Direct damage is minor in soils with more than 12% clay and silt particles <16 µm, although indirect damage by TRV may still occur.

The four species that are most common in the Netherlands differ somewhat in their preference of soil type. *Paratrichodorus teres* is most common on marine calcareous sandy soils in the west of the Netherlands but is also found in the east. *Trichodorus primitivus* is more commonly found on sandy loam soil and sandy silt loam soil in the west and north of the country and along the rivers. *Trichodorus similis* and *P. pachydermus* often occur in mixed populations on wind-deposited sand layers with a high percentage of sand mainly in the east of the country, although *T. similis* is more widespread and is also found in some other areas. The latter two species are the most common trichodorids reported in general from Germany and in particular as pathogens of potato. Regarding soil type, *T. similis* and *P. pachydermus* are mainly reported from loamy sand to silty loam soils. However, a few records also exist from loamy soils.

Symptoms of damage

Typical for an infestation with trichodorids is the occurrence of some plants that grow well in a patch that is otherwise severely damaged (Fig. 45.2). The symptoms of infestation are stubby roots and a root system with a branched or bushy appearance. Trichodorids feed on the epidermal cells just behind the zone of root elongation, causing swelling and stunting of the root tip (Taylor and Brown, 1997). In cases of severe infestation, the root may stop growing, inciting the formation of new roots. Trichodorids in potato also cause above-ground symptoms, where the sprouts start winding and show elongated brown spots (Fig. 45.3). Sprouts can even die off.

Fig. 45.2. A characteristic field symptom of direct damage by trichodorids is the alternation of severely damaged and seemingly unaffected plants in a patch. Photograph courtesy of Wageningen University & Research, Field Crops.

Fig. 45.3. Trichodorids cause swelling and winding of the sprouts and elongated brown spots. Photograph courtesy of Wageningen University & Research, Field Crops.

This symptom can easily be mistaken for an infection with *Rhizoctonia*. Although the multiplication of *P. teres* on potato is lower than that of the other trichodorids, damage to the plant is more severe and potatoes may have a cracked appearance. Regarding virus symptoms, TRV in susceptible potato may cause yellow blotches on the leaves (stem mottle; Fig. 45.4), but the main cause of yield loss in potato is the formation of arcs and/or spots of corky tissue in the tubers as described above. The symptoms are often confused with the deficiency disease caused by a lack of calcium.

Biology and life cycle

Trichodorids are ectoparasites that primarily occur in sandy soils that are prone to drying in periods of drought. However, damage by trichodorids has also been recorded from loamy soils, at least in some regions. Trichodorids can be found in the entire soil layer where roots occur, but often are found around the area where the topsoil meets the subsoil (Cooper and Harrison, 1973). Different species seem to preferably

Fig. 45.4. Stem mottle is the above-ground symptom of potato infected with TRV. Photograph courtesy of Wageningen University & Research, Field Crops.

inhabit different soil depths where some species may even be found at 60–90 cm depth. Trichodorids appear to be susceptible to drought and the distribution over the soil profile is related to time of the year and soil moisture. The concentration in deeper soil layers seems to be due to low survival in the drier upper layer and not so much to migration to deeper soil layers (Rössner, 1972). This probably is the reason why problems with trichodorids and TRV are lower in years with a dry spring, when the density of trichodorids around the roots of the newly planted crop is low. In autumn, the density of trichodorids in the upper soil layer increases again.

All life stages of the nematode are able to acquire and transmit TRV when feeding on infected plant roots, but the virus is lost from the nematode when moulting. Trichodorids are relatively long-lived species with a lifespan of up to 20 weeks that retain virus also in periods without access to TRV infected plants (Taylor and Brown, 1997).

Interactions with other nematodes and pathogens

Trichodorid nematodes can transmit TRV and pea early-browning virus (PEBV). TRV has a very broad host range that includes many crop species and wild plants including weeds, whereas PEBV has only been found in leguminous crops. Different trichodorid species are known to transmit different serologically distinct types of TRV (so-called serotypes), which vary in the ability to multiply in different plant species. TRV may be transmitted through daughter potatoes, although the rate of transmission decreases over generations. TRV may also be transmitted through infested arable weeds and weed seeds that carry the virus. Trichodorids that feed on the infested weeds may acquire the virus and subsequently transmit it to the crop. No interaction with fungi or bacteria is known.

Recommended integrated nematode management (INM)

The INM approach that is advocated in the Netherlands is based on prevention, soil sampling and monitoring, crop rotation and, as a last resort, supplementary measures including nematicides. As it is very difficult to eradicate trichodorids and TRV when they are present in a field, it should be stressed that prevention is important. Prevention starts with the use of certified planting material that has been inspected for diseases, especially TRV. Further, a high level of hygiene on the farm, cleaning machinery before moving from one field to the other, avoids the spread of nematodes among fields. Hygiene also includes weed management, as many arable weed species may be a source of trichodorids and TRV. Weed management is especially important as a long-term strategy, although in the short term it may not decrease virus transmission. Cooper and Harrison (1973) reported that in one experiment, intensive weed management for one and a half years resulted in a higher level of spraing incidence than no weeding. They hypothesized that the nematodes preferably feed on weeds over potato. In the weeded treatment, infested trichodorids that survived the lay period had no alternative than to feed on potato and as a result transferred the virus, but in the unweeded treatment, they may have fed more on the weeds than on the potato plants.

Secondly, knowledge about the field and the nematode species present is important. The soil type may already give information about the probability of problems with trichodorids, which are very unlikely to occur on heavy soils. Some famers have changed their soil texture by ploughing up heavier soil to the surface or by bringing heavy soils from elsewhere. This measure prevents direct damage but does not prevent damage by TRV. The history of the field, including knowledge about problems that occurred in different crops in the past, and observation of irregularities in crop growth are relevant to note. Soil sampling and assessment of the plant parasitic nematodes that are present are essential to create a sound crop rotation. As different trichodorid species vary in host range, determination to species level is advised. With the use of the websites 'Aaltjesschema' (in Dutch) or 'Best4Soil' (22 languages), the most ideal cropping frequency and order can be determined, including the use of green manure crops. The websites contain both information on the rate of multiplication of the nematodes and sensitivity of the crop to damage, as well as additional background information. Considering the broad host range of trichodorids and TRV, designing a crop rotation may be quite challenging. It is important to take into consideration what trichodorid species is present. For example, fodder radish has been found to be successful in the management of *P. teres* and its associated TRV serotype, as both do not multiply on this green manure crop. Similarly, spring barley can be used to suppress *P. teres*-associated TRV, as it does multiply trichodorids, but not the serotype of TRV that is transmitted by *P. teres*. The level of TRV in the field is brought down when the nematodes multiply and juveniles feed on roots that are free from TRV. However, these measures do not hold for other trichodorid species and their associated TRV serotype. Different potato cultivars vary greatly in their sensitivity to TRV. Growth of a tolerant cultivar yields tubers that are free of symptoms but do contain and multiply the virus.

As supplementary measures, fumigant (metam-sodium that degrades into the biological active compound methylisothiocyanate) and non-fumigant nematicides (e.g. oxamyl. fosthiazate and fluopyram) can be used. Application guidelines can vary a lot and thus regional requirements need to be enforced thoroughly. When nematicides are used to suppress other nematodes, trichodorids may also be suppressed as a side effect. The presence of fresh organic matter seems to hamper the transmission of TRV, maybe through decreased nematode activity. However, addition of compost decreases trichodorid numbers to some degree, but does not influence spraing incidence levels. Anaerobic soil disinfestation has not been studied as a specific measure to manage trichodorids, but in the one experiment where they were measured as a side effect, numbers decreased below the detection level after 13 weeks treatment (Goud *et al.*, 2004). However, the occurrence of TRV was not determined in this study. Inundation for 16 weeks decreased numbers of trichodorids to very low levels, but infection with TRV was still found in some samples (Asjes *et al.*, 1996). Because of its insufficient efficacy, inundation is currently not advised as a control measure for TRV in the Netherlands.

Optimization of nematode management

The observation that direct damage by trichodorids is less severe in dry springs has led to the idea that lowering the soil water table around the time of planting may reduce damage. This would need further investigation but is unlikely to solve indirect damage by transmission of TRV. When the distribution of soil texture in a field is not homogeneous, problems with trichodorids may be localized to patches with lighter soil texture. In that case, if deeper soil layers contain more clay and silt particles, deep ploughing of specific patches may change the soil texture so that it becomes unsuitable for trichodorids. This measure has successfully been performed in the Wieringermeer polder, one of the areas that has been reclaimed from the sea.

Knowledge transfer to farmers, advisers and students is important to implement an INM strategy for trichodorids and TRV. With increasing awareness and knowledge about the TRV problem its management will improve. For the most part transfer of knowledge systems are available and are being used.

Future research requirements

The main focus of research in nematology has been on sedentary endoparasitic nematodes and their relationship to the plant, including resistance breeding. Much less is known about the mode of interaction between ectoparasitic nematodes and plants. It remains intriguing why trichodorids are able to infect many plant species, but not all. Further, it would be interesting to study the cause of differences in host plant range among different trichodorid species. This may aid selecting non-hosts or poor hosts for a better trichodorid and/or TRV management. Furthermore, potato cultivars differ in their susceptibility for spraing disease. However, the underlying mechanisms are far from being understood. Thus, it is still unknown if the lower susceptibility of some potato genotypes is the result of a plant resistance response against the nematode or against the virus or more a tolerance response against the virus. An answer to this question might prepare the way for selection towards enhanced resistance and/or tolerance.

Outlook – anticipating future developments

Effects of climate change in north-western and central Europe will lead to milder winters and warmer summers and an increase in total as well as extreme precipitation. As a result of increasing temperatures, plant evaporation and the chance of a water deficit during the growing season will increase. These scenarios may have different implications for the effects of trichodorids and TRV on potato. On the one hand, a drier spring may limit the occurrence of the nematodes to lower soil layers, decreasing the chance that they will affect the newly planted crop. Dry conditions later in the season will reduce crop yield as roots damaged by the nematode are less effective in taking up soil water and nutrients. Furthermore, milder winters may stretch the length of the growing season and thus the period of nematode activity. Overall, the current scenarios discussed in relation to global warming for temperate regions will most likely increase disease incidence and severity.

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