# Occurrence and ecology of trichodorid nematodes in Belgium

Dirk DE WAELE* and August COOMANS

*Instituut voor Dierkunde, Rijksuniversiteit Gent, K.L. Ledeganckstraat 35, 9000 Gent, Belgium.*

SUMMARY

The frequency of occurrence and ecology of trichodorids in Belgium was investigated by examining two thousand and fifteen soil samples. About 20 % of these soil samples contained trichodorid nematodes with *Trichodorus similis* and *Paratrichodorus pachydermus* being the most common species followed by *T. primitivus, T. viruliferus, T. cylindricus, T. variopapillatus, P. teres, T. velatus, T. sparsus* and *P. nanus*. Numerous significant relationships were present between species and the biotopic factors primary vegetation, percent of sand, percent of silt and pH. Trichodorid species common in Belgium and Britain differed in their frequency of occurrence.

RÉSUMÉ

*Fréquence et écologie des nématodes Trichodorides en Belgique*

En vue de l'étude de la fréquence et de l'écologie des nématodes Trichodoridae de Belgique, 2 015 échantillons de sol ont été analysés dont 20 % étaient positifs. Dix espèces de Trichodoridae ont été identifiées, les plus fréquentes étant *Trichodorus similis* et *Paratrichodorus pachydermus*, suivies de *T. primitivus, T. viruliferus, T. cylindricus, T. variopapillatus, P. teres. T. velatus, T. sparsus* et *P. nanus*. La répartition des espèces de Trichodoridae en fonction de la végétation primaire, du type de sol et du pH a été analysée. De nombreuses corrélations significatives entre espèces et facteurs de milieu ont été caractérisées. En ce qui concerne les espèces communes à la Belgique et à la Grande-Bretagne, les fréquences observées dans l'un et l'autre pays sont différentes.

Since 1978, the Centre for the Study of Virus-transmission by Nematodes (CSVN) has periodically investigated the seed - and ware potato fields in Flanders, the main producing area in Belgium, for the presence of tobacco rattle virus (TRV) and trichodorid nematodes. TRV causes spraing or corky ringspot in tubers and stem mottle in stems and leaves of susceptible potato cultivars (Harrison, 1970). The virus is transmitted by at least thirteen nematode species, all belonging to the family Trichodoridae (Lamberti & Roca, 1987). According to the CSVN surveys, 17 to 41.5 % of the seed-potato fields and 22 % of the ware potato fields were infested with at least one trichodorid species (Coolen *et al.*, 1980; Barbez, 1983; De Pelsmaeker & Coomans, 1985). About 20 % of seed and ware potato fields were infested with TRV while the nematodes and the virus occurred together in 14 % of the seed-potato fields and 19 % of the ware potato fields (De Pelsmaeker & Coomans, 1985). The trichodorid species most commonly found in potato fields were *Trichodorus primitivus* and, less frequently, *T. similis* and *Paratrichodorus pachydermus. Trichodorus cylindricus* and *T. viruliferus* were found only occasionally (Barbez, 1983; De Pelsmaeker & Coomans, 1985).

In 1977, a survey of the Trichodoridae and Longidoridae of Belgium was initiated as part of the European Plant Parasitic Nematode Survey and financed by a National Foundation for Scientific Research (Belgium) grant. Geographical distribution maps of trichodorid and longidorid nematodes in Belgium have been published by De Waele and Coomans (1983). In the present paper, the distribution of trichodorid nematodes with respect to primary vegetation, soil texture and pH is reported and discussed. The occurrence and ecology of longidorid nematodes in Belgium was reported separately (De Waele & Coomans, 1990).

## Material and methods

Data were obtained during a national survey of virus-vector nematodes (Trichodoridae and Longidoridae) in Belgium between 1977 and 1982 (De Waele, 1980, 1983). Sampling was based on the 10 km grid system of the Universal Transverse Mercator (UTM) maps. Belgium comprises an area 30 500 km$^2$, consisting of some 300 of these 10 km squares. A standard core sampler (5-cm-diameter) was used to collect at least five

* *Present address : Plant Genetic Systems NV, Jozef Plateaustraat 22, 9000 Gent, Belgium.*

soil samples within each 10 km square from five different vegetation types : arable crops, pastures, grass vegetation at road sides, deciduous and coniferous woodland. Each soil sample consisted of about 2 kg of soil collected within an area of about 20 cm diameter and to a depth of 20-40 cm, according to the vegetation type.

Nematodes were extracted from 100 ml subsamples by the decanting and sieving method of Flegg (1967) followed by the ludox centrifugal-flotation method of Coolen and D'Herde (1977). The extracted nematodes were killed and fixed in hot 4 % formalin. Samples were examined for trichodorids and longidorids under a stereoscopic microscope. Nematodes were transferred to anhydrous glycerin by a modified Seinhorst method (De Grisse, 1969) and mounted between cover slips on aluminium slides for species identification.

Biotopic data collected for each sample were primary vegetation type, soil texture (percent of sand, percent of silt) and pH. Soil texture was determined by a rapid hydrometer method based on Day's (1965) modification of Bouyoucos' (1951) technique. The pH of the soil was measured electrometrically using a Philips PW 9408 digital pH meter.

The data were added to the databank of the European Plant Parasitic Nematode Survey at the Scottish Crop Research Institute, Dundee, Scotland, held at the Edinburg Regional Computer Centre, Scotland, U.K. Chi-squared contingency tests were used to analyse the relationships between the frequency of occurrence of the virus-vector nematodes and the biotopic data recorded. Quantitative data were transformed to qualitative data by prescribing class limits, thus, percent of sand, percent of silt, and pH were grouped into three, five and four classes, respectively.

## Results and discussion

Two thousand and fifteen soil samples from 908 sampling sites were examined for trichodorids. About 20 % of all samples contained at least one species. Ten species were identified, among them the two species previously reported from Belgium (Table 1). As the Belgian survey was organized in the same way as the survey undertaken in Britain (Alphey & Boag, 1976) it was possible to compare the frequency of occurrence and ecology of trichodorid species common to both countries.

The results of the national survey show that trichodorid nematodes are prevalent in Belgium. A comparable infestation level (22 %) was found in Great Britain (Alphey & Boag, 1976) whereas in Italy only 9.6 % of all soil samples collected during a national survey were infested with one or more trichodorid nematode species (Roca & Lamberti, 1984). The species most frequently recorded in the national survey are also very common in potato fields in Belgium and are known to transmit TRV.

Table 1

Trichodorid nematodes found in Belgium during the national survey (1977-1982).

| Nematode species | No. of positive samples | % of total samples (n = 2015) |
|---|---|---|
| *Trichodorus similis* Seinhorst | 169 | 8.4 |
| *Paratrichodorus pachydermus* (Seinhorst) Siddiqi* | 160 | 7.9 |
| *Trichodorus primitivus* (de Man) Micoletzky* | 80 | 4.0 |
| *Trichodorus viruliferus* Hooper | 66 | 3.3 |
| *Trichodorus cylindricus* Hooper | 24 | 1.2 |
| *Trichodorus variopapillatus* Hooper | 15 | 0.7 |
| *Paratrichodorus teres* (Hooper) Siddiqi | 9 | 0.4 |
| *Trichodorus velatus* Hooper | 9 | 0.4 |
| *Trichodorus sparsus* Szczygiel | 5 | 0.2 |
| *Paratrichodorus nanus* (Allen) Siddiqi | 4 | 0.2 |
| All trichodorid nematodes | 394 | 19.6 |

* Species previously reported from Belgium.

*Trichodorus similis, P. pachydermus, T. primitivus* and *T. viruliferus* are also the most frequently recorded species in most continental western European countries (Alphey & Taylor, 1986). The frequency of occurrence of *T. similis* and *P. pachydermus* is about the same in Belgium, the Netherlands and some parts of France (Van Hoof, Maat & Seinhorst, 1967; Seinhorst & Van Hoof, 1982), but in W. Germany and Poland, *P. pachydermus* is more common than *T. similis* (Sturhan, 1967; Wyss, 1969; Rau, 1975; Szczygiel & Brzeski, 1985). In Britain, *T. primitivus* is the most frequently recorded trichodorid species followed by *P. pachydermus* while *T. viruliferus* and *T. similis* occur less frequently (Alphey & Boag, 1976). In southern Europe, *T. viruliferus* is the most common trichodorid in Italy while *P. pachydermus, T. similis* and *T. primitivus* are rare or absent (Roca & Lamberti, 1985). The species which are less common in Belgium also occur less frequently elsewhere in Europe. Outside Belgium, *P. nanus* is know only from Britain, The Netherlands and France (Alphey & Boag, 1976; Seinhorst & Van Hoof, 1982; Scotto la Massèse, 1985) and *T. velatus* from Britain, Poland and France (Alphey & Boag, 1976; Szczygiel & Brzeski, 1985; Scotto la Massèse, 1985). Two species, *T. hooperi* and *P. anemones,* which have been found in Britain (Alphey & Boag, 1976) were not recorded in Belgium.

In general, relatively more populations were associated with grasses at road sides, deciduous woodland and arable crops than with pastures or coniferous woodland (Table 2). Almost 25 % of all samples from grasses at road sides, deciduous woodland and arable crops con-

tained at least one trichodorid species. Fifty percent or more of the *P. nanus* and *T. cylindricus* populations were recovered from grasses at road sides while more than 40 % of the *P. pachydermus* and half of the *T. velatus* populations were associated with deciduous woodland. Twenty to 30 % of the *T. primitivus, T. viruliferus, T. variopapillatus* and *T. similis* populations were recovered from arable crops. Only about 10 to 15 % of the samples from coniferous woodland and pastures contained trichodorids. *Trichodorus similis* was present in 70 % of the infested samples from pastures. *Trichodorus variopapillatus, T. velatus* and *P. teres* were not significantly associated with a vegetation type. In contrast with Belgium, arable crops in Britain supported more trichodorid populations than any other vegetation type : 27 % of all samples from arable crops contained trichodorids compared with 5, 7 and 12 % of all samples from coniferous woodland, pastures and deciduous woodland, respectively (Alphey & Boag, 1976). In Britain, samples from arable land yielded 63 % of all the trichodorid populations recorded compared with 21 % in Belgium.

The association of trichodorids with some arable crops, deciduous tree species and hedgerows is shown in Table 4. About 50 % of all samples collected from maize and 40 % of those from rye were infested with trichodorids. Almost half the number of populations recovered from maize were *T. similis*. Among the deciduous tree species, *Populus* spp., *Acer* spp. and *Betula* spp. were most frequently infested with trichodorids. Fifty percent or more of all *T. variopapillatus* and *T. viruliferus* populations recovered from deciduous woodland were associated with *Populus* spp. Only 15 % of all samples collected from hedgerows contained trichodorids.

In general, relatively more populations were recovered from soils with a high percent of sand and low percent of silt (Table 3). About 40 % of all samples with a sand fraction > 90 % were infested with trichodorids compared with 6 % for samples with a sand fraction < 80 %. Four species, *T. primitivus, T. variopapillatus, T. velatus* and *P. teres* showed no preference for a particular soil type and were not significantly associated with a percent of sand or percent of silt class. All populations of *T. sparsus* and *P. nanus* and most populations of *T. similis, T. cylindricus, P. pachydermus* and *T. viruliferus* were associated with soils with a sand fraction > 90 % and a silt fraction < 10 %. Forty-four percent of the soils with a silt fraction of 20 % or higher contained *T. primitivus*. In Britain, trichodorids were also most frequently found in sandy loam to sandy soils : about 50 % of the samples with trichodorids had a sand fraction higher than 80 % and a silt fraction lower than 10 % (Alphey & Boag,

Table 2

Association of *Trichodorus* and *Paratrichodorus* species with vegetation type in Belgium.

| Nematode species | No. of samples with nematodes | | | | | Statistical significance* |
|---|---|---|---|---|---|---|
| | Vegetation type | | | | | |
| | Arable crops (n = 341) | Pastures (n = 521) | Grasses at road sides (n = 390) | Deciduous woodland (n = 539) | Coniferous woodland (n = 89) | |
| *T. cylindricus* | 3 | 6 | 12 | 3 | 0 | * |
| *T. primitivus* | 17 | 13 | 28 | 21 | 1 | ** |
| *T. similis* | 51 | 56 | 34 | 26 | 2 | *** |
| *T. sparsus* | 0 | 3 | 0 | 2 | 0 | — |
| *T. variopapillatus* | 4 | 1 | 4 | 6 | 0 | NS |
| *T. velatus* | 1 | 0 | 2 | 5 | 1 | NS |
| *T. viruliferus* | 15 | 20 | 22 | 9 | 0 | ** |
| *P. nanus* | 0 | 1 | 4 | 0 | 0 | — |
| *P. pachydermus* | 20 | 29 | 36 | 71 | 4 | *** |
| *P. teres* | 1 | 2 | 2 | 3 | 1 | NS |
| All trichodorid nematodes | 75 | 81 | 99 | 128 | 11 | *** |
| % of positive samples | 22.0 | 15.5 | 25.4 | 23.7 | 12.4 | |

* Statistical significances of chi-squared contingency tests applied to the association : *, **, *** : $P < 0.05$, $P < 0.01$, $P < 0.001$, respectively; NS = not significant.

Table 3

Association of *Trichodorus* and *Paratrichodorus* species with soil texture and pH in Belgium.

| Nematode species | No. of samples with nematodes | | | Statistical significance* | No. of samples with nematodes | | | | | Statistical significance* | No. of samples with nematodes | | | | Statistical significance* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | % sand | | | | % silt | | | | | | pH | | | | |
| | 0-79 (n = 587) | 80-89 (n = 762) | 90-100 (n = 639) | | 0-4 (n = 304) | 5-9 (n = 519) | 10-14 (n = 466) | 15-19 (n = 303) | 20- (n = 396) | | 0.5-5.4 (n = 497) | 5.5-6.4 (n = 543) | 6.5-6.9 (n = 408) | 7.0-8.5 (n = 564) | |
| *T. cylindricus* | 2 | 4 | 18 | *** | 10 | 8 | 4 | 1 | 1 | ** | 0 | 7 | 7 | 10 | * |
| *T. primitivus* | 17 | 31 | 32 | NS | 10 | 25 | 23 | 11 | 11 | NS | 12 | 22 | 16 | 30 | NS |
| *T. similis* | 7 | 38 | 124 | *** | 64 | 76 | 20 | 5 | 4 | *** | 66 | 61 | 28 | 14 | *** |
| *T. sparsus* | 0 | 0 | 5 | — | 4 | 1 | 0 | 0 | 0 | — | 3 | 1 | 1 | 0 | — |
| *T. variopapillatus* | 6 | 3 | 6 | NS | 0 | 6 | 3 | 2 | 4 | NS | 1 | 3 | 5 | 6 | NS |
| *T. velatus* | 2 | 4 | 3 | NS | 2 | 2 | 1 | 2 | 2 | NS | 0 | 3 | 2 | 4 | NS |
| *T. viruliferus* | 1 | 9 | 56 | *** | 33 | 28 | 3 | 1 | 1 | *** | 24 | 22 | 9 | 11 | * |
| *P. nanus* | 0 | 0 | 4 | — | 3 | 1 | 0 | 0 | 0 | — | 2 | 1 | 0 | 1 | — |
| *P. pachydermus* | 3 | 34 | 123 | *** | 64 | 73 | 16 | 6 | 1 | *** | 83 | 50 | 12 | 15 | *** |
| *P. teres* | 0 | 4 | 5 | NS | 2 | 3 | 4 | 0 | 0 | NS | 2 | 4 | 2 | 0 | NS |
| All trichodorid nematodes | 37 | 103 | 254 | *** | 131 | 151 | 62 | 25 | 25 | *** | 142 | 112 | 62 | 78 | *** |
| % of positive samples | 6.3 | 13.5 | 39.7 | | 43.1 | 29.1 | 13.3 | 8.3 | 6.3 | | 28.6 | 20.6 | 15.2 | 13.8 | |

* Statistical significances of chi-squared contingency tests applied to the associations; *, **, *** : $P < 0.05$, $P < 0.01$, $P < 0.001$, respectively : NS = not significant.

Table 4

Association of *Trichodorus* and *Paratrichodorus* species with some arable crops, deciduous tree species and hedgerows in Belgium.

| Nematode species | Arable crops | | | | Deciduous tree species | | | | | | | Hedgerows |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Barley (n = 43) | Maize (n = 101) | Rye (n = 15) | Feeder crops (n = 76) | *Acer* spp. (n = 19) | *Alnus* spp. (n = 35) | *Betula* spp. (n = 16) | *Fagus* spp. (n = 104) | *Quercus* spp. (n = 159) | *Populus* spp. (n = 87) | *Salix* spp. (n = 17) | *Crataegus* spp. (n = 61) |
| *T. cylindricus* | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 |
| *T. primitivus* | 2 | 7 | 1 | 1 | 2 | 2 | 1 | 2 | 4 | 5 | 0 | 1 |
| *T. similis* | 4 | 23 | 2 | 7 | 1 | 3 | 1 | 0 | 5 | 7 | 2 | 2 |
| *T. sparsus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *T. variopapillatus* | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 |
| *T. velatus* | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 2 |
| *T. viruliferus* | 1 | 6 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 5 | 1 | 1 |
| *P. nanus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *P. pachydermus* | 2 | 9 | 1 | 2 | 3 | 1 | 3 | 13 | 27 | 10 | 1 | 1 |
| *P. teres* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 |
| All trichodorid nematodes | 10 | 49 | 6 | 12 | 7 | 8 | 5 | 17 | 39 | 34 | 4 | 9 |
| % of positive samples | 23.3 | 48.5 | 40.0 | 15.8 | 36.8 | 22.9 | 31.3 | 16.3 | 24.5 | 39.1 | 23.5 | 14.8 |

1976). Almost 40 % of all *T. primitivus* populations were found in soils with a silt fraction of 20 % or higher compared with 16 % for *P. pachydermus* (Alphey & Boag, 1976).

In general, relatively more populations occurred in soils with a pH < 5.5 (Table 3). Almost 30 % of these soils were infested with trichodorids. In soils with a pH of 5.5 or higher the observed frequency was lower than expected : 20.6 *vs* 27 %, 15.2 *vs* 20.2 % and 13.8 *vs* 28 % in soils with a pH of 5.5 to 6.4, 6.5 to 6.9 and 7.0 to 8.5, respectively. The pH had no discernable effect on *T. primitivus, T. variopapillatus, T. velatus* and *P. teres.* Thirty-six percent or more of the *T. viruliferus, T. similis, P. nanus, P. pachydermus* and *T. sparsus* populations were recovered from soils with a pH < 5.5 whereas half of the *P. teres* populations occurred in soils with a pH between 5.5 and 6.4. About 40 % of the *T. primitivus, T. variopapillatus, T. cylindricus* and *T. velatus* populations were found in soils with a pH > 7. In Britain, only 6.5 % of the soils with a pH < 5.5 and 12.4 % of the soils with a pH between 5.5 and 6.4 were infested with trichodorids whereas 16.9 % of the soils with a pH of 6.5 or higher contained at least one trichodorid species (Alphey & Boag, 1976). Sixty-one percent of all *P. pachydermus* populations and 41 % of all *T. primitivus* populations were found in soils with a pH < 5.5 and pH > 6.5, respectively (Alphey & Boag, 1976).

The results of the national survey indicate that Belgium and Britain initially have had a similar trichodorid nematofauna as has also been demonstrated for longidorids (Topham *et al.,* 1986; De Waele & Coomans, 1990). However, whereas the most frequent longidorid species were the same in both countries, this was not so with the trichodorid species. Differences in species associations of trichodorids between Belgium and Britain have been reported previously (Topham *et al.,* 1986). In Belgium, the degree of association was greatest between *T. viruliferus, T. similis* and *P. pachydermus* whereas in Britain, *P. teres* and *T. cylindricus* were most commonly associated. As in longidorids, the observed ecological differences between populations of the same trichodorid species in Belgium and Britain indicate differences in adaptation to changing habitats. The comparison of the trichodorid and longidorid nematofaunas in Belgium and Britain indicates that trichodorids were more rapid or successful to colonize suitable habitats than longidorids. Of the two types of survival strategies, *r* and *K*, trichodorids with their smaller size, shorter life span and faster multiplication rate can be considered *r* strategists compared with longidorids. In contrast with *K* strategists, *r* strategists are able to rapidly colonize and exploit new favourable environments. However, under Scottish conditions and compared with other nematodes, *T. primitivus* and *P. pachydermus* were considered *K* strategists by Boag and Alphey (1988). Are the trichodorids now *r* or *K* survival strategists? As Norton (1978) emphasized, caution must be employed as to relate these terms to populations of plant-parasitic nematodes.

Cluster analysis has shown that both in Belgium and Britain associations between trichodorid species were closer than between longidorid species (Topham *et al.,* 1986). As a possible explanation the preference of trichodorids for sandy soils has been put forward. Our results confirm the correlation between trichodorid infestations and sandy soils (Winfield & Cooke, 1974; Alphey & Boag, 1976; Barbez, 1983).

When the data obtained during the national survey were compared with the available data on the presence of *T. primitivus, T. similis* and *P. pachydermus* in potato fields some differences were noticed. In potato fields, *T. primitivus* was the most common trichodorid species (Barbez, 1983; De Pelsmaeker & Coomans, 1985) whereas during the national survey, *T. similis* was the most common trichodorid species found. Results from the present study suggest that *T. primitivus,* although found less frequently than *T. similis,* is more tolerant of different biotopic factors. Similar results have been found by Barbez (1983) and De Pelsmaeker and Coomans (1985). However, this cannot explain the greater presence of *T. primitivus* in potato fields since the area in which potatoes are cultivated offers a biotope suitable for *T. similis. Trichodorus similis* was the species most frequently found during the national survey, which included samples from a wide range of biotopes. The influence of sampling method can also be excluded because both species have similar depth distributions, occurring between 0-40 cm (De Pelsmaeker, Calus & Coomans, 1986). Conversely, *T. viruliferus,* which has been found almost as frequently as *T. primitivus* during the national survey, rarely occurred in potato fields (Barbez, 1983; De Pelsmaeker & Coomans, 1985). Otherwise, the optimum biotope for *T. viruliferus* was similar to that for *T. primitivus, T. similis* and *P. pachydermus* (De Waele, 1983). *Trichodorus viruliferus* was found most frequently in the northern part of the country, in the " Polders ", " Vlaamse Zandstreek " and " Kempen " (86.4 % of all *T. viruliferus* populations were found below 50 m altitude); under almost any primary vegetation type (*T. viruliferus* was however absent in coniferous woodland); in soils with a sand fraction > 90 % and a silt fraction < 10 %; mostly at pH values < 6.5. During the national survey, *T. viruliferus* was the species which occurred most often together with other trichodorid species, mostly with *T. primitivus, T. similis* and *P. pachydermus* (81.8 % of all samples in which *T. viruliferus* occurred consisted of mixed populations). These observations suggest that potato is a good host for *T. primitivus* but not for *T. viruliferus.*

ACKNOWLEDGEMENTS

The authors thank Drs T. Alphey and P. Topham, Scottish Crop Research Institute, for advice and help with the statistical

analyses, and the Edinburgh Regional Computing Centre for computer facilities. Special thanks are due to R. van Driessche, A. van Bost, H. van de Wiele and G. Sirejacob (Rijksuniversiteit Gent, Belgium) for technical assistance. The authors acknowledge grant No. 32.0024.77 from the National Foundation for Scientific Research, Belgium.

REFERENCES

ALPHEY, T. J. W. & BOAG, B. (1976). Distribution of trichodorid nematodes in Great Britain. *Ann. appl. Biol.*, 84 : 371-381.

ALPHEY, T. J. W. & TAYLOR, C. E. (1986). *European Atlas of the Longidoridae and Trichodoridae.* Dundee, Scotland, Scott. Crop Res. Inst., 123 p.

BARBEZ, D. (1983). The distribution of virus-vector nematodes in seed-potato fields of Flanders (Belgium) and its relation to some biotic and abiotic factors. *Meded. Fac. Landbouwwet. Rijksuniv. Gent*, 48 : 401-415.

BOAG, B. & ALPHEY, T. J. W. (1988). Influence of interspecific competition on the population dynamics of migratory plant-parasitic nematodes with *r* and *K* survival strategies. *Revue Nématol.*, 11 : 321-326.

BOUYOUCOS, G. J. (1951). Recalibration of the hydrometer method for making mechanical analysis for soil. *Agron. J.*, 23 : 434-438.

COOLEN, W. A., DECREAMER, W., HENDRICKX, G. J. & DE MEYER, P. (1980). Voorkomen en verspreiding van virusoverdragende nematoden in de West en Oostvlaamse pootaardappelenverbouwende gebieden. *Landbouwtijdschrift*, 2 : 333-337.

COOLEN, W. A. & D'HERDE, C. J. (1977). Extraction de *Longidorus* et *Xiphinema* spp. du sol par centrifugation en utilisant du silice colloidal. *Nematol. medit.*, 5 : 195-206.

DAY, P. R. (1965). Particle fractioning and particle size analysis. In : Black, C. E., Evans, D. D., White, J. L., Ensminger, L. A. & Clark, F. E. (Eds) *Methods of soil analysis*, American Society of Agronomy : 547-567.

DE GRISSE, A. T. (1969). Redescription ou modification de quelques techniques utilisées dans l'étude des nématodes phytoparasitaires. *Meded. Fac. Landbouwwet. Rijksuniv. Gent*, 34 : 351-359.

DE PELSMAEKER, M. & COOMANS, A. (1985). Virusoverdragende nematoden in de aardbein-, aardappel- en hopteelt. *Biol. Jaarb. Dodonea*, 53 : 16-30.

DE PELSMEAKER, M., CALUS, A. & COOMANS, A. (1986). Vertical distribution of trichodorids and TRV. *Meded. Fac. Landbouwwet. Rijksuniv. Gent.*, 50 : 769-775.

DE WAELE, D. (1980). Objectives, methods and preliminary results concerning a survey of virus-vector nematodes in Belgium. *Meded. Fac. Landbouwwet. Rijksuniv. Gent*, 45 : 807-813.

DE WAELE, D. (1983). *Geographical distribution and ecology of Trichodoridae and Longidoridae (Nematoda) in Belgium, with a taxonomical study of the genus* Trichodorus *Cobb, 1913.* Ph. D. Thesis, State Univ. Gent, 468 p.

*Accepté pour publication le 14 février 1990.*

DE WAELE, D. & COOMANS. A. (1983). Distribution of Longidoridae and Trichodoridae. In : Alphey, T. J. W. (Ed.) *Atlas of Plant-Parasitic Nematodes of Belgium.* Dundee Scotland, Scottish Crop Research Institute, 42 p.

DE WAELE, D. & COOMANS, A. (1990). Occurrence and ecology of longidorid nematodes in Belgium. *Revue Nématol.*, 13 : 197-202.

FLEGG, J. J. M. (1967). Extraction of *Xiphinema* and *Longidorus* species from soil by a modification of Cobb's decanting and sieving technique. *Ann. appl. Biol.*, 60 : 429-437.

HARRISON, B. D. (1970). Tobacco Rattle Virus. *C.M.I./A.A.B. Descr. Pl. Vir.* No. 12, 4 p.

NORTON, D. C. (1978). *Ecology of plant-parasitic nematodes.* New-York, John Wiley & Sons, XIV + 268 p.

RAU, J. (1975). *Das vorkommen Virusüberträgender Nematoden in ungestörten Biotopen Niedersachsens.* Diss. Techn., Univ. Hannover, 169 p.

ROCA, F. & LAMBERTI, F. (1984). Trichodorids (Nematoda) from Italy. *Nematol. medit.*, 12 : 95-118.

ROCA, F. & LAMBERTI, F. (1985). Distribution of Longidoridae, Xiphinemidae and Trichodoridae. In : Alphey, T. J. W. (Ed.). *Atlas of Plant Parasitic Nematodes of Italy.* Dundee, Scotland, Scott. Crop Res. Inst., 44 p.

SCOTTO LA MASSÈSE, C. (1985). Distribution of Longidoridae, Xiphinemidae and Trichodoridae. In : Alphey, T. J. W. (Ed.). *Atlas of Plant Parasitic Nematodes of France.* Dundee, Scotland, Scott. Crop Res. Inst., 43 p.

SEINHORST, J. W. & VAN HOOF, H. A. (1982). Distribution of Longidoridae, Trichodoridae and Xiphinemidae. In : Alphey, T. J. W. (Ed.). *Atlas of Plant Parasitic Nematodes of The Netherlands.* Dundee, Scotland, Scott. Crop Res. Inst., 33 p.

STURHAN, D. (1967). Vorkommen von *Trichodorus* Arten in Westdeutschland. *Mitt. Biol. Bund Anst. Ld-u. Forstw.*, 121 : 146-150.

SZCZYGIEL, A. & BRZESKI, M. W. (1985). Distribution of Longidoridae, Xiphinemidae and Trichodoridae. In : Alphey, T. J. W. (Ed.). *Atlas of Plant Parasitic Nematodes of Poland.* Dundee, Scotland, Scott. Crop. Res. Inst., 32 p.

TOPHAM, P., ALPHEY, T. J. W., BOAG, B. & DE WAELE, D. (1986). Comparison between plant-parasitic nematode species associations in Great Britain and in Belgium. *Nematologica*, 31 : 458-467.

VAN HOOF, H. A., MAAT, D. Z. & SEINHORST, J. W. (1967). Some data on the presence of tobacco rattle virus and its vectors in France. *Meded. Fac. Landbouwwet. Rijksuniv. Gent.*, 32 : 939-947.

WINFIELD, A. L. & COOKE, D. A. (1975). The ecology of *Trichodorus.* In : Lamberti, F., Taylor, C. E. & Seinhorst J. W. (Eds) *Nematode Vectors of Plant Viruses.* London, New-York, Plenum Press : 309-341.

WYSS, U. (1969). Untersuchungen über das Schadauftreten wandernder Wurzelnematoden an Erdbeerkulturen in Niedersachsen. *Mitt. biol. Bundanst. Ld-u. Forstw.*, 36 : 110-126.