Influence of interspecific competition on the population dynamics of migratory plant-parasitic nematodes with r and K survival strategies

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SUMMARY

Samples taken over a five year period at a field site in which the dominant plant-parasitic nematode species were *Rotylenchus robustus, Trichodorus primitivus* and *Paratrichodorus pachydermus* indicated that the nematodes had K survival strategies. They had relatively low rates of multiplication and their numbers showed no obvious seasonal cycling. In soil where their numbers had been greatly reduced following treatment with the fumigant dichloropropene, numbers of a fourth species *Paratylenchus nanus,* initially present in small numbers, rapidly increased. This species had an r survival strategy, its numbers increasing rapidly in the absence of competition and also showing marked seasonal fluctuations. In non-fumigated soil *P. nanus* numbers remained low, probably due to interspecific competition, especially with *R. robustus.*

RÉSUMÉ

Influence de la compétition interspécifique sur la dynamique des populations de nématodes phytoparasites migrateurs ayant des stratégies de survie de types « r » et « K »

Des prélèvements effectués pendant cinq années dans un champ où les espèces dominantes de nématodes phytoparasites étaient *Rotylenchus robustus, Trichodorus primitivus* et *Paratrichodorus pachydermus,* permettent d'attribuer à ces nématodes une stratégie de survie de type « K ». Leur taux de multiplication est relativement faible et ils ne montrent pas de cycle saisonnier net. Dans les sols où les populations de ces nématodes ont été drastiquement réduites par application d'un nématicide fumigant (dichloropropène), une quatrième espèce, *Paratylenchus nanus,* voit son taux, initialement faible, croître rapidement. Cette espèce a une stratégie de survie de type « r », le nombre de ses individus croissant rapidement en l'absence de compétition et les fluctuations saisonnières de sa population étant bien marquées. Dans les sols non traités avec un nématicide fumigant, le taux de *P. nanus* reste faible, ceci étant probablement dû à la compétition interspécifique, *R. robustus* semblant plus particulièrement en cause.

The role of competition in limiting insect and mammal populations is well documented but its influence in regulating nematode populations has received little attention and is less well understood. Boag (1986) demonstrated that intraspecific competition limited the maximum population density of *Rotylenchus robustus* populations under perennial crops and Seinhorst (1965) developed his yield response curves from the competition models of Nicholson (1933). Interspecific competition has been demonstrated under laboratory conditions (Johnson, 1970; Kraus-Schmidt & Lewis, 1981) but there are few examples recorded from field situations (Bird, Brooks & Perry, 1974). The population dynamics of competing parasitic animals has recently been reviewed (Dobson, 1985) and Adamson (1985) has commented upon the r and K strategies of nematode parasites of millipedes. In this paper the effect of interspecific competition on field populations and the survival strategies of the plant parasitic nematodes *R. robustus, Trichodorus primitivus, Paratrichodorus pachydermus* and *Paratylenchus nanus* are reported.

Materials and methods

The data in this paper are from a series of ecological studies which examined the effect of different host crops on the population dynamics of *R. robustus* and trichodorid nematodes at a Scottish forest nursery site. Details of the experimental design and procedure have already been published (Alphey, 1985; Boag, 1986). At the site one half of each experimental plot was fumigated with dichloropropene (92 % a.i. as Telone II) at 207 l/ha applied by hand injector gun at a depth of 20 cm. The other half of each plot was untreated. After four weeks and aeration by rotary cultivation, each plot was sown with perennial ryegrass/white clover *(Lolium perenne/ Trifolium repens)* mixture.

Composite soil samples were taken at various depths (Tab. 2) every two months between May 1980 and July 1985. Sampling points were marked to avoid resampling. After mixing, 200 g subsamples were soaked in water overnight (Simons, 1973) and nematodes extracted using a modified sieving and decanting technique, heat

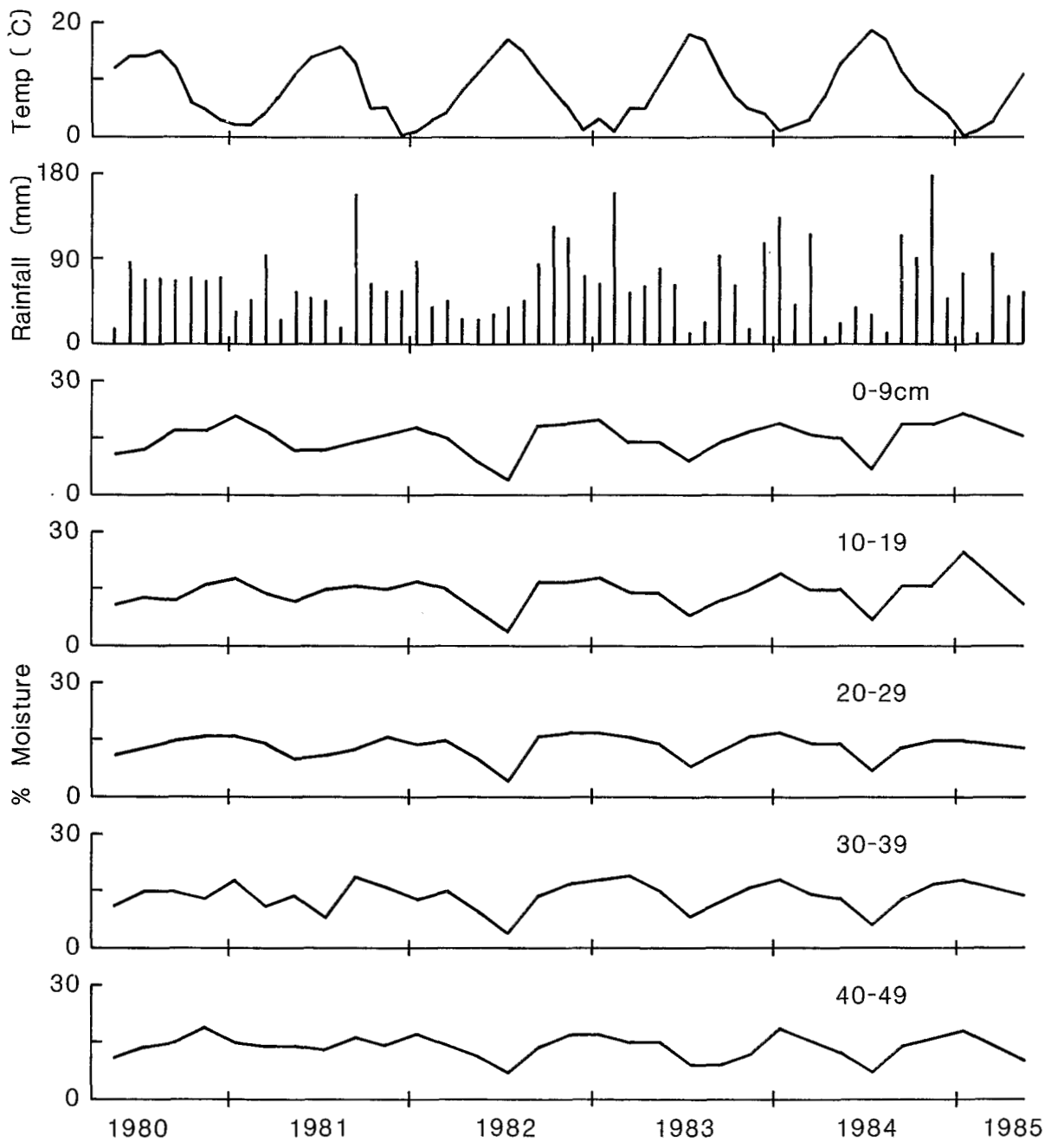

Fig. 1. Temperature and rainfall measurements from the Scottish Crop Research Institute, Invergowrie and percentage soil moisture content from samples taken under grass/clover sward at the forest nursery.

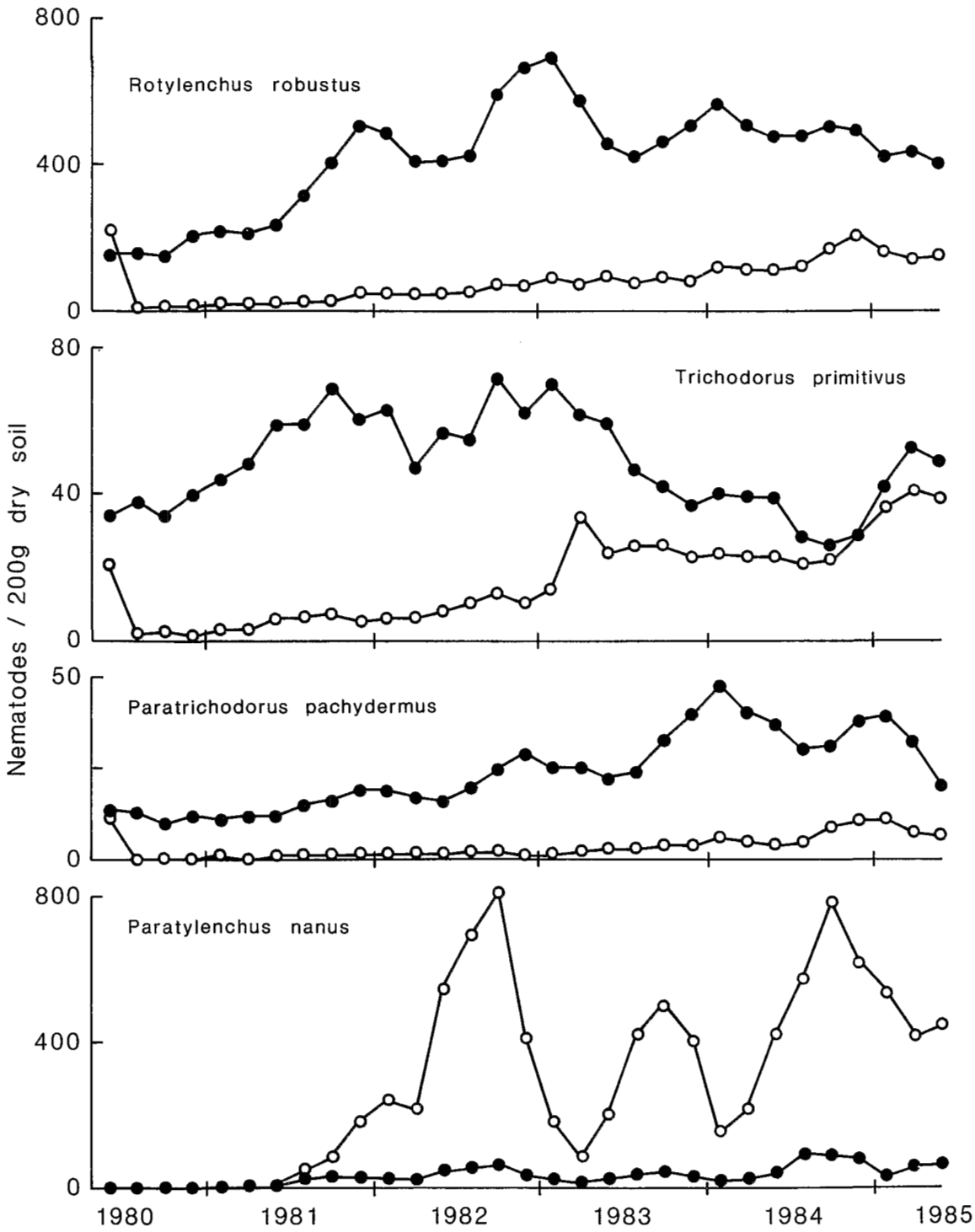

Fig. 2. Variation in mean nematode numbers (0,50 cm) May 1980 to May 1985, ○, fumigated; ●, non-fumigated.

killed, fixed, stored and counted as described by Boag (1974). Nematodes expressed as numbers per 200 g dry soil were transformed to (x + 1) for statistical analysis,

Observations showed that meteorological data periodically recorded at the nursery was very similar to that routinely recorded at the meteorological site of the Scottish Crop Research Institute (Boag, 1982) and consequently the latter data are used in this paper.

The occurrence of nematophagous fungi, which may have limited nematode populations was tested for in 1984 using the soil sprinkling technique described by Duddington (1955). *Panagrellus redivivus* was used as the target organism because it has been shown to stimulate the predatory activity of a wide range of nematophagous fungi (Jansson & Norbring-Hertz, 1980). Preliminary identification of the fungi found was made using the key of Cooke and Godfrey (1964) and subsequently confirmation was made by staff at the Commonwealth Mycological Institute, Kew.

Results

Between 1980 and 1985 there was no consistent seasonal pattern in the monthly rainfall data but seasonal fluctuations in temperature and percentage soil moisture content were observed. Low soil moisture levels, of 8 % (pF 3.8) (Boag, 1982) in July 1982 and July 1984 and surface temperatures below — 23° in January 1982 did not decrease the numbers recovered of any of the nematode species under study (Figs 1 & 2).

Prior to fumigation in 1980 the most abundant plant-parasitic species were *R. robustus* (229/200 g soil), *T. primitivus* (31/200 g soil) and *Paratrichodorus pachydermus* (14/200 g soil). *Paratylenchus nanus* was extremely scarce (< 0.2/200 g soil). Subsequently the grass mixture was shown to be a good host for *R. robustus*, *T. primitivus* and *P. pachydermus*, their numbers progressively increasing over the first 2-3 years in the non-fumigated subplots (Fig. 2). Although their numbers declined later, they were still greater after five years than at the start of the experiment in May 1980 (Tab. 1). Dichloropropene reduced the numbers of *R. robustus*, *T. primitivus* and *P. pachydermus* by 94-96 % between May and July 1980 (Fig. 2). The small residual populations survived and increased throughout the duration of the experiment but their annual rate of increase was small and never exceeded × 2.25 (Tab. 1). Consequently, after five years the populations of *R. robustus* and *Paratrichodorus pachydermus* hed still not attained the initial 1980 population levels.

The population density of *Paratylenchus nanus* at the site was initially very low and was further decreased to below the detectable level by fumigation. It was not until 1982 that the species was again detected in all plots. Numbers of *P. nanus* increased little in the non-fumigated plots whereas in the fumigated plots they increased rapidly. In the first two years following fumigation annual multiplication rates were *c.* × 7 and × 184 (Tab. 1). Numbers of *P. nanus* also exhibited marked seasonal fluctuations with the highest numbers being recorded in the autumn and the lowest numbers in early spring.

Table 1

Comparison of the rates of multiplication of *Rotylenchus robustus*, *Trichodorus primitivus*, *Paratrichodorus pachydermus* and *Paratylenchus nanus* in fumigated and non-fumigated plots growing grass between May 1980-May 1985 (mean numbers of nematodes 200 g dry soil, depth 0-50 cm)
(Figures in parenthesis refer to mean yearly percentage population increases or decreases over that of the previous year)

Date	R. robustus		T. primitivus		P. pachydermus		P. nanus	
	Fumigated	*Non Fumigated*	*Fumigated*	*Non Fumigated*	*Fumigated*	*Non Fumigated*	*Fumigated*	*Non Fumigated*
Initial population May 1980	226	231	21	40	12	15	0.1	0.2
July 1980-May 1981	13 (— 94)	180 (— 22)	2.0 (— 95)	41 (3)	0.5 (— 95)	11 (— 27)	0.8 (700)	3.3 (1 550)
July 1981-May 1982*	37 (185)	404 (124)	6.5 (225)	58 (41)	1.0 (100)	16 (45)	148 (18 400)	25 (658)
July 1982-May 1983*	76 (105)	587 (45)	14 (115)	67 (16)	1.8 (80)	25 (56)	446 (201)	37 (48)
July 1983-May 1984*	103 (36)	482 (— 18)	25 (79)	40 (— 41)	4.5 (150)	36 (44)	360 (— 19)	31 (— 16)
July 1984-May 1985*	160 (55)	467 (— 3)	31 (24)	40 (0)	7.5 (67)	32 (— 11)	601 (67)	75 (142)
Overall effect**	1 131	159	1 450	— 2	1 400	191	75 025	2 170

* Yearly counts comprise mean counts for July, September, November, January, March and May.
** Overall effect refers to the percentage population increase or decrease between the year of July 1980-May 1981 and July 1984-May 1985.

A study of the depth distribution of the four species indicated that *T. primitivus* and *Paratrichodorus pachydermus* were generally found at greater depths than *R. robustus* and *Paratylenchus nanus* which were more abundant in the top 20 cm of soil (Tab. 2). The depth distribution of the two trichodorid species were significantly correlated ($r = 0.946$, D. F. = 3) and that between *R. robustus* and *P. nanus* was highly significant ($r = 0.979$, D. F. = 3).

Table 2

Depth distribution of *Rotylenchus robustus*, *Trichodorus primitivus*, *Paratrichodorus pachydermus* and *Paratylenchus nanus* [mean nematode numbers (May 1980-May 1985)/200 g dry soil]

Depth (cm)	R. robustus	T. primitivus	P. pachydermus	P. nanus
0-9	435 (35) *	36 (22)	16 (23)	321 (38)
10-19	384 (31)	42 (26)	18 (26)	316 (38)
20-29	226 (18)	42 (26)	19 (28)	138 (17)
30-39	126 (10)	26 (16)	10 (14)	37 (4)
40-49	79 (6)	17 (10)	6 (9)	25 (3)

* Figures in parenthesis refer to the percentage of the nematodes found at that depth.

Two nematophagous fungi, *Arthrobotrys oligospora* (Frss.), and *Monacrosporium bembicoides* (Drechsler) were detected at the site. The fungi were found in both fumigated and non-fumigated sub-plots in May 1984.

Discussion

The factors responsible for the marked increase in numbers of *P. nanus* in the dichloropropene treated sub-plots and not in the untreated sub-plots are not fully understood. There is no evidence to suggest differential susceptibility of any of the nematode species to dichloropropene. Dichloropropene has some fungicidal action (Buczacki & White, 1979) and initially it was suspected that it may have reduced the population of nematophagous fungi thereby allowing the residual populations of *P. nanus* to increase. However, this is now considered unlikely as both *A. oligospora* and *M. bembicoides* were detected from the fumigated as well as the non-fumigated sub-plots. If nematophagous fungi had been a major predator limiting populations of *P. nanus* then a marked decrease in the nematode numbers would have been expected as the fumigated plots became recolonised by fungi. However, there was no evidence of this occurring. The depth distribution of *P. nanus* and of *R. robustus* were similar and the crops grass and clover are known to be a good hosts for both nematode species (Rössner, 1971; Coursen, Rohde & Jenkins, 1958). Furthermore, studies using plants growing in agar (Rhoades & Linford, 1961; Klinkenberg, 1963; Boag, 1980) have shown that both these species feed in a similar manner ectoparasitically on the root epidermis and root hairs. Therefore, although it cannot be proved it seems probable that competition between the two species, occupying similar ecological niches, was the main factor preventing numbers of *P. nanus* increasing in the non-fumigated sub-plots. Once competition from *R. robustus* had been removed in the fumigated sub-plots *P. nanus* numbers increased rapidly. The density of *P. nanus* population in the fumigated plots was probably regulated by seasonal variation in the availability of food and by intraspecific competition.

This study also demonstrated the difference in survival strategies of the nematode species. Two types of survival strategies in animals have been described by Southwood (1981). K strategists tend to be large animals with slow multiplication rates and are not readily able to exploit changes in environmental conditions. In contrast r strategists are small animals with fast multiplication rates giving them the ability to rapidly colonise and exploit new favourable environments. *R. robustus*, *T. primitivus* and *Paratrichodorus pachydermus* had relatively low rates of multiplication, even when initial populations were small. Under Scottish conditions, the low rates of multiplication, relative stability in population infrastructures and lack of any marked seasonal fluctuation of numbers of these nematodes (Boag, 1981; Boag, 1982; Alphey, 1985) are characteristics which identify them as K survival strategists. These characteristics contrast strongly with those of *Paratylenchus nanus* a nematode which, when competition was reduced, exhibited high multiplication rates and marked seasonal fluctuations in its numbers — the characteristics of an organism with a r survival strategy. In the non-fumigated sub-plots numbers of *P. nanus* were suppressed and remained low due to interspecific competition from the many *R. robustus* which acted in an imperfectly density-dependent manner (Milne, 1984).

These results show that fumigant nematicides, such as dichloropropene, can give long-term control of K survival strategy nematodes, but that these chemicals can also allow other pathogenic species with r survival strategies such as *P. nanus* (Winfield, 1985) to multiply rapidly.

References

ADAMSON, M. L. (1985). Rhizonematida (Nematoda) of *Rhinocricus bernardinensis* (Rhinocricidae; Spriobolida; Diplopoda) with comments on r- and K-selection in nematode parasties of diploids. *Revue Suisse Zool.*, 92 : 871-896.

ALPHEY, T. J. W. (1985). A study of spatial distribution and population dynamics of two sympatric species of trichodorid nematodes. *Ann. appl. Biol.* 107 : 497-509.

BIRD, G. W., BROOKS, O. L. & PERRY, C.E. (1974). Dynamics of concomitant field populations of *Hoplolaimus columbus* and *Meloidogyne incognita*. *J. Nematol.*, 6 : 190-194.

BOAG, B. (1974). Nematodes associated with forest and woodland trees in Scotland. *Ann. appl. Biol.*, 77 : 41-50.

BOAG, B. (1980). Observations of temperature on rates of feeding of the plant-parasitic nematodes *Rotylenchus robustus*, *Xiphinema diversicaudatum* and *Hemicycliophora conida*. *J. Nematol.*, 12 : 193-195.

BOAG, B. (1981). Observations on the population dynamics and vertical distribution of trichodorid nematodes in a Scottish forest nursery. *Ann. appl. Biol.*, 98 : 463-469.

BOAG, B. (1982). Observations on the population dynamics, life cycle and ecology of the plant-parasitic nematode *Rotylenchus robustus*. *Ann. appl. Biol.*, 100 : 157-165.

BOAG, B. (1986). The influence of host and intra-specific competition in controlling populations of the plant parasitic nematode *Rotylenchus robustus* (Nematoda : Hoplolaimidae). *Nematologica*, 31 (1985) : 344-351.

BUCZACKI, S. T. & WHITE, J. G. (1979). The value of soil sterilants for the control of clubroot on a field scale. *Pl. Path.*, 28 : 36-39.

COOKE, R. C. & GODFREY, B.E.S. (1964). A key to the nematode destroying fungi. *Trans. Br. mycol. Soc.*, 34 : 322-331.

COURSEN, B. W., ROHDE, R. A. & JENKINS, W. R. (1958). Additions to the host lists of the nematodes *Paratylenchus profectus* and *Trichodorus christiei*. *Pl. Dis. Reptr*, 42 : 456-460.

DOBSON, A. P. (1985). The population dynamics of competition between parasites. *Parasitology*, 91 : 317-347.

DUDDINGTON, C. L. (1985). Notes on the technique of handling predaceous fungi. *Trans. Br. mycol. Soc.*, 38 : 97-103.

JANSSON, H. B. & NORDBRING-HERTZ, B. (1980). Interaction between nematophagous fungi and plant-parasitic nematodes : attraction, induction of trap formation and capture. *Nematologica*, 26 : 383-389.

JOHNSON, A. M. (1970). Pathogenicity and interaction of three nematode species and six Bermuda grasses. *J. Nematol.*, 2 : 36-41.

KLINKENBERG, C. H. (1963). Observations on the feeding habits of *Rotylenchus robustus*, *Pratylenchus crenatus*, *P. penetrans*, *Tylenchorhynchus dubius* and *Hemicyliophora similis*. *Nematologica*, 9 : 502-506.

KRAUS-SCHMIDT, H. & LEWIS, S. A. (1981). Dynamics of concomitant populations of *Hoplolaimus columbus*, *Scutellonema brachyurum* and *Meloidoygne incognita* on cotton. *J. Nematol.*, 13 : 41-48.

MILNE, A. (1984). Fluctuations and natural control of animal populations, as exemplified in the garden chafer *Phyllopertha horticola* (L.). *Proc. Roy. Soc. Edinburg*, 82 B : 145-199.

NICHOLSON, A. J. (1933). The balance of animal populations *J. Anim. Ecol.*, 2 : 132-178.

RHOADES, H. L. & LINFORD, M. B. (1961). A study of the parasitic habit of *Paratylenchus projectus* and *P. dianthus*. *Proc. helminth. Soc. Wash.*, 28 : 185-190.

RÖSSNER, J. (1971). Untersuchungen zur Entwicklung von *Rotylenchus robustus*. *Nematologica*, 17 : 255-261.

SEINHORST, J. W. (1965). The relationship between nematode density and damage to plants. *Nematologica*, 11 : 137-154.

SIMONS, W. R. (1973). Nematode survival in relation to soil moisture. *Meded. LandbouwHogesch., Wageningen*, 73 : 1-85.

SOUTHWOOD, T. R. E. (1981). Bionomic strategies and population parameters. In : May, R. M. (Ed.). *Theoretical ecology, principles and applications*, Oxford, Blackwell Scientific Publications : 30-52.

WINFIELD, A. L. (1985). Observations on the pin nematode *Paratylenchus nanus*, a possible pest of glasshouse lettuce *Lactuca sativa*. *Crop Res.*, 25 : 3-12.

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