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# Host Range Assessment of *Helicotylenchus pseudorobustus* (Tylenchida: Hoplolaimidae) on Pasture Species

L. T. Davis, N. L. Bell, R. N. Watson, and T. C. Rohan

*Abstract:* The host status of 15 commonly occurring pasture species for *Helicotylenchus pseudorobustus* was tested in a greenhouse trial. Only tall fescue, with and without *Neotyphodium* endophyte infection, was a good host (Pf/Pi = final/initial population > 1). Inoculation survival was tested in a second trial, which showed that only 10% of the *H. pseudorobustus* nematodes survived the first 7 days after inoculation. When the Pf/Pi was adjusted to account for a 10% survival, all of the grass and clover hosts tested had a Pf/Pi > 1. Both trials showed a positive correlation between increased numbers of *H. pseudorobustus* and free-living nematodes.
*Key words: Helicotylenchus pseudorobustus,* host range, pasture species, spiral nematode, free-living nematodes.

The spiral nematode *Helicotylenchus pseudorobustus* is a soil-dwelling migratory ectoparasitic or semi-endoparasitic nematode that feeds on plant roots (Fortuner, 1985). This nematode has been found in soils beneath pastures and turf throughout New Zealand (Yeates and Wouts, 1992) and has been associated with a wide range of plants including grasses, legumes, and tree species (Churchill and Ruehle, 1971; McGawley and Chapman, 1983; Yeates, 1984; Yeates and Wouts, 1992). Damage attributed to *H. pseudorobustus* has been reported in soybean (*Glycine max*) (Elmiligy and Norton, 1973), turf (Chastagner and McElroy, 1984; Feldmesser and Golden, 1974; Todd and Tisserat, 1990), and cotton (*Gossypium hirsutum*) seedlings in association with Fusarium wilt (Ma et al., 1994). New Zealand pastures on high fertility soils are based predominantly on perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) with tall fescue (*Festuca arundinacea*) as a major alternative grass. *Neotyphodium* endophyte-infected ryegrass and tall fescue plants, which exhibit increased resistance to insect feeding compared to endophyte-free plants, are commonly sown into New Zealand pastures; however, their effect on plant-parasitic nematodes is varied (Van Heeswijck and McDonald, 1992).

The endoparasitic nematodes under pasture in northern parts of New Zealand include *Meloidogyne hapla, M. trifoliophila, Heterodera trifolii,* and *Pratylenchus* spp. *Meloidogyne* and *Heterodera* infect only legumes, whereas *Pratylenchus* invade both grass and legume roots. The dominant ectoparasitic or semi-endoparasitic nematodes present in these pastures include species of *Helicotylenchus, Paratrichodorus,* and *Paratylenchus* (Mercer and Watson, 1996). The host range of *Paratylenchus nanus* and *Paratrichodorus minor* has been reported by Bell and Watson (2001a).

The objectives of this study were to determine the host status of some commonly occurring pasture plants for *H. pseudorobustus,* and the survival rate of this nematode immediately after inoculation into soil.

## Materials and Methods

The *H. pseudorobustus* isolate used in these experiments was collected from an experimental plot of tall fescue (cv. Advance) infected with endophyte *Neotyphodium* sp. (strain AR501) near Kerikeri, Northland, in October 2001 and maintained on endophyte-infected tall fescue plants in the greenhouse.

All nematode extractions or checks for the presence of nematodes were carried out using a modification of the Whitehead and Hemming tray method (Bell and Watson, 2001b). Briefly, soil was placed on nested tissue paper and coarse mesh in a 26×21×6-cm plastic tray filled with 500 ml of tap water and left to extract for 72 hours, after which the nematode suspension volume was reduced by sequential settling and aspiration in 1 liter, 150-ml and 10-ml beakers. As a proportion of the nematodes extracted over a 144-hour timespan, this method extracts 80% to 85% of mobile nematodes (Bell and Watson, 2001b).

*Host range:* A total of 15 plant species were tested as potential hosts (Table 1), a fallow control was included, and each was replicated five times. All seed was provided by the Margot Forde Forage Germplasm Centre, Palmerston North. Each plant species was subjected to two treatments, with and without nematodes, to determine the impact of the inoculated level of *H. pseudorobustus* on root weight. In late August 2002, individual plants were grown from seed in PVC tubes (30-mm diam., 200-mm length) with a sealed base. Each tube was filled with 100 g of Horotiu sandy loam (Vitric Hapludand) soil that had been microwaved in 500-g lots for 3 minutes on high power (700 W) to kill the nematodes present in the soil. A 200-g subsample of microwaved soil was examined to confirm efficacy of treatment, and no nematodes were extracted. The nutrients for plant growth were provided by an initial application of 1 g/tube of slow-release fertilizer (18N : 2.1P : 9.1K) (Osmocote Scotts-Sierra Horticultural Products, Marysville, OH). Tubes were inoculated with approximately 120 nematodes (72 juveniles and 48 adult females, juvenile/female = 1.5) and suspended in 1 ml of tap water

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AgResearch, Private Bag 3123, Hamilton, New Zealand.
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E-mail: lee.davis@agresearch.co.nz
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TABLE 1. List of the plant species tested as potential hosts for *Helicotylenchus pseudorobustus,* along with their accession number from the Margot Forde Forage Germplasm Centre.

| Common name | Botanical name | Cultivar | Accession No. |
|---|---|---|---|
| Annual poa | *Poa annua* L. | Dwarf Blue | BP1495 |
| Brown top | *Agrostis capillaris* L. | Grasslands Muster | BR1408 |
| Cocksfoot | *Dactylis glomerata* L. | Grasslands Wana | K2620 |
| Italian ryegrass | *Lolium multiflorum* Lam. | Concord | B3687 |
| Paspalum | *Paspalum dilatatum* Poir. | Grasslands Raki | BO303 |
| Perennial ryegrass | *Lolium perenne* L. | Yatsyn 1 | A8263 |
| Perennial ryegrass[a] | *L. perenne* L. | Yatsyn 1 (Wild type[c]) | A11602 |
| Tall fescue | *Festuca arundinacea* Schreb. | Grasslands Advance | T2509 |
| Tall fescue[b] | *F. arundinacea* Schreb. | Grasslands Advance (AR501[c]) | T6296 |
| Caucasian clover | *Trifolium ambiguum* Bieb. | Endura | AZ4195 |
| Red clover | *T. pratense* L. | Grasslands Colenso | F2657 |
| Subterranean clover | *T. subterraneum* L. | Bacchus Marsh | AK518 |
| White clover | *T. repens* L. | Grasslands Huia | C19739 |
| Plantain | *Plantago lanceolata* L. | Grasslands Lancelot | O1138 |
| Yarrow | *Achillea millefolium* L. | Grassland Yarrow | O1098 |
| Fallow | Control | — | — |

[a] *Neotyphodium lolli* endophyte-infected cultivar.
[b] *Neotyphopdiium coenophialum* endophyte-infected cultivar.
[c] Endophyte strain identification.

2 weeks after sowing. The inoculum was pipeted into a 3-mm-wide, 10-mm-deep hole made next to each seedling. The inoculum included approximately 825 free-living nematodes/ml.

The tubes were placed in a water bath at 20 °C and watered to 70% of the water holding capacity for 58 (rep 1), 82 (rep 2), 86 (rep 3), 92 (rep 4), or 99 (rep 5) days after inoculation (DAI). Plant foliage was trimmed to a height of 100 mm 58 days after inoculation and subsequently at 14-day intervals. At harvesting, nematodes were extracted from all the soil and roots in each tube, after which the roots were washed free of soil and dried for 48 hours at 80 °C and the weight recorded.

Nematodes were counted using a light microscope. The rate of reproduction was calculated as Pf/Pi (final population/initial population or inoculum) and the J/F (juvenile/female) ratio. Plants examined were classified as excellent hosts (if Pf/Pi > 10), good hosts (if 10 > Pf/Pi > 1), maintenance hosts (if Pf/Pi is close to 1), and poor hosts (Pf/Pi < 1) according to definitions provided by Ferris et al. (1993).

All statistical analyses were performed using Genstat for Windows (7th edition, VSN International Ltd., Hemel Hempsted, UK). Three separate two-way analysis of variances were performed using plant species and presence of nematodes as independent variables. Dependent variables were untransformed root dry weight data and $\log_e$-transformed Pf/Pi and J/F ratios. Pearsons product moment correlation was calculated for the relationship between Pf/Pi and J/F in this trial, and between abundance of *H. pseudorobustus* and free-living nematodes in both trials.

*Inoculation mortality:* Due to low *H. pseudorobustus* numbers recorded in the host range test at 58 days, a test was conducted in March 2003 to determine the survival of *H. pseudorobustus* immediately after inoculation into soil. The protocol was the same as for the host range test but contained only one plant species, endophyte-infected tall fescue. There were two treatments; tubes with or without tall fescue plants were inoculated with approximately 120 *H. pseudorobustus* nematodes (101 juveniles and 19 adult females, J/F = 5.3) suspended in 1 ml tap water. The inoculum included approximately 67 free-living nematodes/ml.

The numbers of nematodes at 7, 14, 28, and 56 days after inoculation were recorded from five replicates of each treatment at each harvest. A two-way analysis of variance was performed, defining the dependent variable as $\log_e$ transformed J/F and treatment and day as independent variables.

## RESULTS

*Host range: Helicotylenchus pseudorobustus* did not affect root dry weights with the exception of yarrow, which had a higher root weight recorded for inoculated plants ($P < 0.05$) (Table 2). Only the grass tall fescue (endophyte-free and infected) had a Pf/Pi > 1, with annual poa and paspalum having a Pf/Pi close to 1. The plantain, yarrow, Caucasian, and subterranean clover had the lowest Pf/Pi values of the plants tested. Live *H. pseudorobustus* nematodes were still found in the fallow treatment 99 DAI. Greater mean Pf/Pi values were recorded on perennial ryegrass infected with wild type *Neotyphodium lolii* than on the endophyte-free plants (Table 2). Pf/Pi values were correlated positively with J/F ratios ($r = 0.73$) with the exceptions being paspalum, which had a relatively large Pf/Pi value but a small J/F ratio, and endophyte-free perennial ryegrass, which had a small Pf/Pi value and a large J/F ratio. *Helicotylenchus pseudorobustus* numbers increased generally through time on good hosts (Fig. 1). At 58 DAI, the

TABLE 2. Root dry weights, reproduction rates (Pf/Pi), and juvenile-to-female ratios (J/F) of *Helicotylenchus pseudorobustus* for the host-range test.

| | Root dry weight (g) | | | | | | |
|---|---|---|---|---|---|---|---|
| Common name | without nematodes | with nematodes | SED[a] | Pf/Pi[b] | SEM[c] | J/F | SEM[c] |
| Annual poa | 0.49 | 0.55 | 0.11 | 0.98 (9.8) | 0.27 | 12.7 | 3.65 |
| Brown top | 1.34 | 1.29 | 0.22 | 0.68 (6.8) | 0.11 | 12.2 | 1.97 |
| Cocksfoot | 1.20 | 1.36 | 0.17 | 0.29 (2.9) | 0.07 | 5.6 | 2.19 |
| Italian ryegrass | 1.41 | 1.50 | 0.29 | 0.35 (3.5) | 0.11 | 6.3 | 2.25 |
| Paspalum | 0.84 | 1.16 | 0.21 | 0.84 (8.4) | 0.23 | 3.6 | 1.17 |
| Perennial ryegrass | 1.26 | 1.58 | 0.14 | 0.23 (2.3) | 0.06 | 8.3 | 2.46 |
| Perennial ryegrass[d] | 1.56 | 1.42 | 0.21 | 0.67 (6.7) | 0.22 | 11.1 | 4.45 |
| Tall fescue | 0.60 | 0.83 | 0.24 | 1.77 (17.7) | 0.42 | 12.1 | 3.27 |
| Tall fescue[d] | 0.99 | 0.74 | 0.35 | 1.53 (15.3) | 0.39 | 11.4 | 2.67 |
| Caucasian clover | 0.56 | 0.53 | 0.12 | 0.14 (1.4) | 0.05 | 3.1 | 1.22 |
| Red clover | 0.31 | 0.64 | 0.20 | 0.47 (4.7) | 0.13 | 2.7 | 0.84 |
| Subterranean clover | 0.90 | 1.10 | 0.23 | 0.13 (1.3) | 0.04 | 2.8 | 0.68 |
| White clover | 0.65 | 0.54 | 0.16 | 0.69 (6.9) | 0.16 | 4.8 | 1.14 |
| Plantain | 0.97 | 0.91 | 0.18 | 0.09 (0.9) | 0.03 | 1.4 | 1.80 |
| Yarrow | 1.35 | 1.51 | 0.05* | 0.08 (0.8) | 0.06 | 2.7 | 1.22 |
| Fallow | — | — | — | 0.05 (0.5) | 0.01 | 1.5 | 3.90 |

[a] Standard error of the difference.
[b] Adjusted Pf/Pi in brackets to account for 10% survival post inoculation observed in Trial 2.
[c] Standard error of the mean.
[d] *Neotyphodium* endophyte-infected cultivars.
* $P < 0.05$.

mean Pf/Pi value was 0.22 for the four best hosts rising to 2.18 at 99 DAI. The greatest number of *H. pseudorobustus* nematodes from a single tube (536) was recorded on endophyte-free tall fescue. There was a positive correlation ($r$ = 0.79) between the number of *H. pseudorobustus* and free-living nematodes across all treatments.

*Inoculation mortality:* The survival rate of *H. pseudorobustus* at 7 DAI was only 10% for both treatments (Fig. 2). Nematode numbers on the tall fescue treatment increased over the 56 DAI, whereas mean nematode numbers decreased from 12 to 6 on the fallow treatments. There were significantly more nematodes on the tall fescue than on the fallow treatment at 28 ($P < 0.05$) and 56 ($P < 0.001$) DAI. For both treatments the mean J/F ratio at each of the 4 harvest times remained close to the initial ratio of 5.3 (Table 3). The number of free-living nematodes increased over the duration of the experiment for the endophyte-infected tall fescue treatment, whereas in the fallow numbers reached a plateau at day 28 (Fig. 3). There were significantly more free-living nematodes on the tall fescue than on the fallow treatment on day 56 (P < 0.001). There was a correlation ($r$ = 0.67, $P$ = 0.001) between the increas-

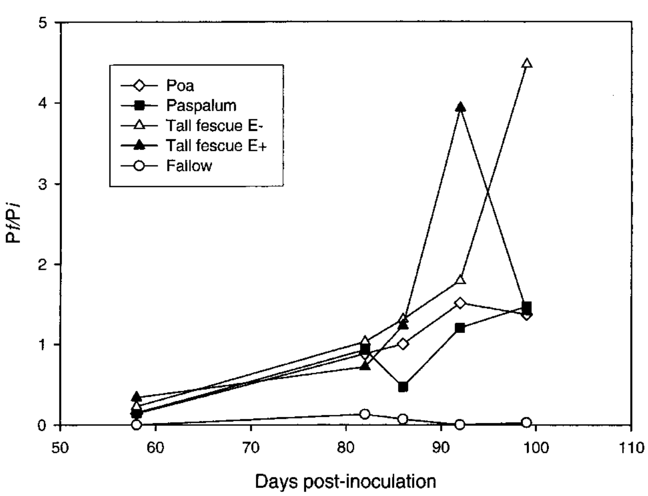


FIG. 1. The Pf/Pi of *Helicotylenchus pseudorobustus* for the four best host species and the fallow control for each replicate. Pf/Pi = the final nematode population divided by the initial inoculum. E− and E+ represent tall fescue with and without the endophyte *Neotyphodium*, respectively.

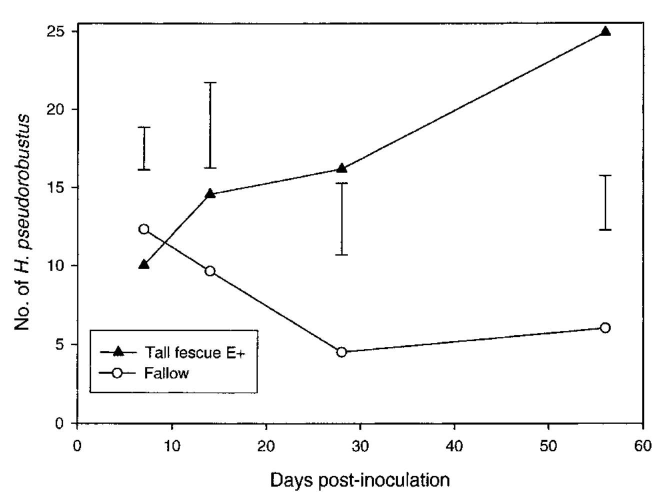


FIG. 2. Population density changes of *Helicotylenchus pseudorobustus* in tubes of endophyte-infected tall fescue or fallow tubes, after inoculation with 120 mixed-age *H. pseudorobustus*. Symbols are back-transformed means ($n$ = 5), and bars represent the back-transformed standard error of the difference.

TABLE 3. The mean juvenile-to-female ratios (J/F) of *Helicotylenchus pseudorobustus* for the two treatments, endophyte-infected tall fescue and fallow control. The mean ($n = 5$) and standard error of the difference values (SED) are back-transformed.

| Days after inoculation | Tall fescue E+[a] J/F | Fallow J/F | SED |
|---|---|---|---|
| 0 | 5.3 | 5.3 | — |
| 7 | 4.8 | 4.6 | 1.9 |
| 14 | 5.7 | 4.6 | 2.1 |
| 28 | 5.1 | 2.7 | 1.6 |
| 56 | 5.9 | 3.7 | 2.0 |

[a] *Neotyphodium* infected.

ing number of total *H. pseudorobustus* and free-living nematodes for the endophyte-infected tall fescue treatment, but no correlation was observed for the fallow treatment ($r = -0.39$).

As a comparison of *H. pseudorobustus* populations on endophyte-infected tall fescue between the two trials, in the host range test 41 *H. pseudorobustus* nematodes were recorded at 58 days (replicate 1), whereas in the mortality test (Trial 2) there were 25.4 (range of 21 to 36) *H. pseudorobustus* at 56 days. The mean Pf/Pi at 58 DAI for the endophyte-infected tall fescue treatment in the host range test was 0.34, whereas in the mortality test at 56 days for the tall fescue treatment Pf/Pi was 0.21. The J/F ratio at 58 days for the endophyte-infected tall fescue (1.2) was similar to the initial J/F (1.5) in the host-range trial, as was the case in the mortality trial.

Using the 10% survival determined in the motality test to adjust the P*f*/P*i* values in the host-range test (Table 2), tall fescue with and without endophyte were excellent hosts for *H. pseudorobustus* (Pf/Pi > 10). The remaining eight grasses and red and white clover were good hosts (10 > Pf/Pi > 1). Caucasian clover, subterranean clover, plantain, and yarrow were categorized as maintaining hosts (Pf/Pi values close to 1).

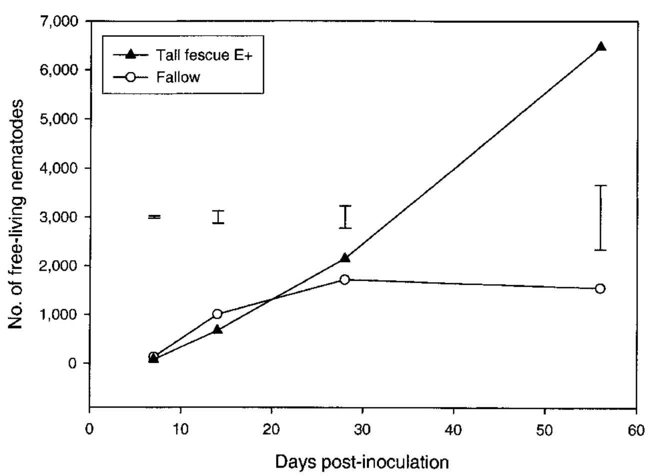


FIG. 3. Population density changes of free-living nematodes in tubes of endophyte-infected tall fescue or fallow tubes, after inoculation with 67 nematodes. Symbols are back-transformed means ($n = 5$), and bars represent the back-transformed standard error of the difference.

## DISCUSSION

The most susceptible hosts for *H. pseudorobustus* in this study were grass species, particularly tall fescue. From the time the first replicate was dismantled at 58 DAI until the last replicate at 99 DAI, the four best hosts were tall fescue (endophyte-free and infected), annual poa and paspalum, and the hosts brown top, perennial ryegrass (endophyte-infected), and white clover exhibited a general increase in nematode numbers. With the exception of paspalum and white clover, these species exhibited high J/F ratios. Trudgill (1995) found that when a species of nematode fed on a favorable host, the population was dominated by juveniles resulting in a high J/F ratio.

The Pf/Pi values are comparable to those found in studies by Townshend and Potter (1976) and Talavera and Nava (2002), in which host-range tests for *H. digonicus* were conducted on pasture and cereal species. Townshend and Potter (1976) found *H. digonicus* population increases were considerably lower than for *Paratylenchus projectus* and *Pratylenchus* species. Similarly, the Pf/Pi values observed here for *H. pseudorobustus* are considerably lower than those of *Paratylenchus nanus, Paratrichodorus minor* (Bell and Watson, 2001a), and *Pratylenchus neglectus* and *P. thornei* (Vanstone and Russ, 2001a, 2001b) in host-range studies involving pasture species grown in similar conditions and time periods. This indicates that reproductive rate for *Helicotylenchus* species is slower than these other plant-parasitic nematodes on pasture and cereal species. McGawley and Chapman (1983) reported that females of *H. pseudorobustus* took 50 days to increase in number on soybeans. Similarly, Churchill and Ruehle (1971) observed an increase in the number of *H. pseudorobustus* females on sycamore (*Platanus occidentalis*) hosts after only 3 months.

Similar numbers and Pf/Pi values of *H. pseudorobustus* were found in the endophyte-infected tall fescue treatment for both trials, indicating nematode reaction to the experimental setups were analogous. The mortality test indicated a survival rate of only 10% of the initial inoculum. Assuming this was also the case for the host-range test, all the grass and clover species tested in this trial would have a Pf/Pi > 1. The mortality caused by inoculation is not generally considered in host-range or cultivar tests. Seven papers have appeared in this journal in the last 4 years that cited Pf/Pi values (and (or) reproductive rates) for trials using vermiform nematode stages as part of their inoculum (Castillo and Vovlas, 2002; Forge et al., 2000; Nico et al., 2003; Robbins et al., 2000, 2001, 2002; Silva and Inomoto, 2002), but none have mentioned inoculum survival. The high mortality rate observed in the current study was unexpected, and any future host-range trials will involve determination of inoculation survival as part of our protocol.

The presence of *Neotyphodium* endophyte in tall fescue and perennial ryegrass has variable responses against plant nematodes (Van Heeswijck and McDonald, 1992). In this study, the presence of endophyte in tall fescue and perennial ryegrass did not appear to be a deterrent to feeding by *H. pseudorobustus,* and in the case of perennial ryegrass greater numbers were observed on endophyte-infected plants. Kimmons et al. (1990) also found that presence of endophyte had no effect on *H. pseudorobustus* numbers in tall fescue. Cook et al. (1991) reported that populations of plant-parasitic nematodes were not reduced on endophyte-infected perennial ryegrass plants and that in two out of three field sites the numbers actually increased. They attributed this increase in nematode abundance to greater root weight of endophyte-infected ryegrass. In this study, however, there was no difference in root dry weight between endophyte-free and endophyte-infected plants.

Both current trials showed a positive correlation between increased numbers of *H. pseudorobustus* and free-living nematodes. This is expected, as feeding by a plant-parasitic nematode would result in nutrient leaching from plant roots and increasing numbers of microbes, resulting in an enhanced abundance of microbial feeding nematodes. Several publications report low amounts of root herbivory by plant-parasitic nematodes, below the damage threshold for white clover, resulted in an increase in total microbial biomass (Denton et al., 1999; Yeates et al., 1999). *Helicotylenchus pseudorobustus* numbers in this test did not reach a level sufficient to cause plant-growth suppression. In the mortality test, an increase in free-living nematodes was observed in the fallow control until day 28, but this was not related to *H. pseudorobustus* numbers. Microwaving soil can cause an increase of available nitrogen (Wright et al., 1989), and nitrogen addition has been shown to increase numbers of free-living nematodes (Ettema et al., 1999).

*Helicotylenchus pseudorobustus* nematodes were still present in the fallow control 99 DAI, which concurs with research by Churchill and Ruehle (1971), who reported survival of this species in soil for 9 months without a host. Other nematode genera from the Hoplolaimidae family, such as *Hoplolaimus* and *Rotylenchus,* have been found to survive for similar time periods in fallow soil (Rhoades, 1984; Rhoades and Forbes, 1986; Seinhorst, 1968) and have relatively low rates of multiplication (Boag and Alphey, 1988; Boag and Neilson, 1996). These characteristics are a probable reason why *Helicotylenchus* has been found to be a poor colonizer after soil sterilization (Yeates and van der Meulen, 1996) and prefers sites of more mature successional status (Villenave et al., 2001)

The Pf/Pi ratios adjusted according to survival rate after inoculation suggest that *H. pseudorobustus* has a wide host range and this, together with its persistence in the absence of a host plant, could make this nematode difficult to remove from the soil. Regular crop rotation between host and non-host species may provide an effective means of managing *H. pseudorobustus* by keeping nematode numbers low rather than removing them completely. Estimates of the damage threshold of *H. pseudorobustus* are needed, as studies have suggested that relatively large populations (>4,000 nematodes/plant or 100 $cm^3$ of soil) of *Helicotylenchus* are necessary to cause economical damage to hosts (Elmiligy and Norton, 1973; Yeates, 1980), and these densities have been reported in New Zealand pasture (Yeates, 1984).

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