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# Interactions between *Heterodera avenae* and *Pratylenchus neglectus* on Wheat[1]

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*Abstract:* In a long-term field experiment, differential population densities of *Heterodera avenae* were produced by frequent cropping with resistant (cv. Panema) or susceptible (cv. Peniarth) oat. The two oat cultivars were equally good hosts of *Pratylenchus neglectus* in a glass house experiment with field soil. On wheat crops grown after oats in field experiments, *P. neglectus* population densities in roots were higher in plots where *H. avenae* had been controlled than in plots with moderate infestations (40 *H. avenae* eggs/g soil). The field observations indicated that the reduction in population densities of *P. neglectus* coincided with the development in roots of sedentary stages of the cyst nematode. Evidence for an indirect effect of *H. avenae* on *P. neglectus* was found in vitro in a split-root experiment. In the same field, grain yields of two wheat cultivars susceptible or resistant to *H. avenae,* but both susceptible to *P. neglectus,* was not reduced by *P. neglectus.* Alternation of *H. avenae* resistant and susceptible cultivars is a possible way of exploiting the inverse relationship between these nematodes, whilst controlling cyst nematode populations in intensive cereal production systems.

*Key words: Avena sativa, Heterodera avenae,* integrated management, interspecific interaction, long-term experiment, nematode, pathogenicity, population dynamics, *Pratylenchus neglectus,* resistance, split-root, *Triticum aestivum.*

The cereal cyst nematode, *Heterodera avenae* Wollenweber, the root-knot nematode, *Meloidogyne naasi* Franklin, and root-lesion nematodes, *Pratylenchus spp.*, are the main soil-borne parasitic nematodes associated with economic damage to cereals in France (1). In the case of the two former species, rotations and resistant cultivars represent the most attractive control measures (2,11). Applications of nematicides are not economical on cereals and are decreasing in frequency due to ecological considerations (18).

In long-term field experiments using cultivars of spring barley and oat resistant to *H. avenae,* it has been observed that densities of *Pratylenchus neglectus* Rensch (=*P. minyus* Sher and Allen) increased where *H. avenae* was suppressed (3). *Pratylenchus spp.* and *M. naasi* were also negatively correlated on winter wheat (6). In interspecific relationships between sedentary and migratory nematodes (5), the close nematode–host relationship established by the sedentary species may make the host either more or less suitable for the latter. Thus, *M. incognita* suppressed *P. brachyurus* on soybean (8), and *P. penetrans* on tomato (7). In contrast, *M. naasi* stimulated *P. penetrans* on bentgrass (20).

The present study used experimentally induced differential infestations of *H. avenae* obtained by the frequent use of resistant (cv. Panema) or susceptible (cv. Peniarth) oat in a long-term experiment from 1982–1990. Winter wheat was grown on the site; the effects of *H. avenae* infection on the development of the root system (13), plant growth, and wheat production (15) were studied, and observations were made on remote sensing by thermal infrared radiation of hydric disturbances caused by the nematode (9). The trial was designed to provide information on cereal nematodes of crops grown under farm conditions. This necessitated that it be designed within constraints imposed by available land, time, and seed supplies. In particular, the need to prevent soil and seed movement between rotations in farm management practices was crucial. To this end, we adopted simple design to produce a large-scale trial capable of maintenance on the farm. Our present study had three ob-

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jectives: 1) to assess the effect of long-term use of oat cultivars with resistance to *H. avenae* on the population dynamics of *P. neglectus;* 2) to evaluate the interaction between these two nematode species in vitro in a split-root experiment; and 3) to measure the pathogenicity of *P. neglectus* to winter wheat.

## MATERIALS AND METHODS

*Population dynamics of P. neglectus in the field:* The population densities of *H. avenae* (pathotype Ha11) and *P. neglectus* in wheat roots were studied from 1990 to 1992 on the site of a long-term experiment carried out in the Argentan Plain (Normandie, France) on a uniform calcareous soil (13). The experiment consisted of three pairs of adjacent 360 $m^2$ (6 × 60 m) blocks (A, B, and C) in which *H. avenae* densities had been adjusted by previous cropping to above or below the damage threshold of 5 to 10 juveniles per g soil (13,14). Cereals were grown in accordance with local farming practices. Plant samples from half blocks were taken by digging all the plants in two adjacent 0.5-m lengths of row (0.2 $m^2$), at five points 10 m apart, along the middle of each half block. Nematodes in washed and weighed root samples were extracted by maceration in a blender followed by centrifugation and flotation in a 1.18 specific gravity sugar solution (4). Nematodes were extracted from the whole root sample before tillering, and from a 10 g subsample of roots thereafter.

In the first experiment, two blocks were sown with the early maturing winter wheat cv. Fidel (Block A) and the later maturing cv. Arminda (Block B) on 27 October 1989. In 1990, the densities of *H. avenae* and *P. neglectus* in roots were estimated at one node (Feekes scale 6) and flowering (Feekes scale 10-5-3). In the second field experiment, Block C was sown with cv. Arminda in successive seasons (27 October 1990 and 12 November 1991). Nematode population densities were estimated in monthly samples from September 1990 through June 1992, except for February and July to October, 1991.

Data in each set of observations were log10 $(x + 1)$ transformed and subjected to analysis of variance performed with the SAS program (19). Percentages of eggs in the total population (females + juveniles + eggs) were arcsine transformed before statistical analysis. Means were classified according to the Newman-Keuls test at $P \leq 0.05$.

*Reproduction of P. neglectus on two oat cultivars:* In the field experiments, the differential population densities of *H. avenae* were produced largely by growing two winter oat cultivars, resistant cv. Panema and susceptible cv. Peniarth. The host status of these two cultivars for *P. neglectus* was determined in a glasshouse experiment. Field soil from Block C with low *H. avenae* infestations was collected; *P. neglectus* population densities in this soil were 1,652 ± 491/100 g soil. Four replicates of two 3-day old seedlings/760 ml soil of each oat cultivar were sown in pots and grown at 20 C and a 16-hour photoperiod for 72 days. Nematodes from a 5-g sample of roots from each pot were counted, and data were analyzed by the procedures described for the field experiments.

*Split-root experiment: Heterodera avenae* (pathotype Ha 41) second-stage juveniles (J2) were obtained from cysts reared in 1991 on wheat cv. Lutin and placed in water at 8 C for emergence. *Pratylenchus neglectus* were extracted by elutriation from the Argentan soil (Block C with low *H. avenae* infestation) sampled in October 1991, and females were selected and stored at 3 C before inoculation. Seeds of cv. Arminda were disinfected with 0.02% $HgCl_2$ in 95% absolute alcohol for 5 minutes, rinsed with sterile water, and germinated at 23 C. Single 3-day old seedlings were put on agar (2%) in petri plates divided into two compartments (A and B) with a notch made in the divider with a soldering iron, under sterile conditions. The seedlings were placed in the notch and the root system was separated into two halves, one half in each compartment. Roots were fixed to the surface of the agar with agar blocks and inoculated with the following nematode treatments: 24 *P. neglectus* (*Pn*) in A + 24 *Pn* in B; 24 *Pn* + 8 *H. avenae* (*Ha*); and 8 + 8 *Ha*. These treatments were based on observations of the optimum inocula for in vitro reproduction (12; Lasserre, unpubl.). Nematodes were inoculated under the root tip. Plants were grown at 18 ± 1 C and under a 16-hour light regime. Treatments were replicated as shown in Table 5. Fifty days after inoculation, females of *H. avenae* were collected and counted and roots stained with acid fuchsin (4 mg of fuchsin in 50% absolute alcohol and 50% acetic acid) to estimate *P. neglectus* densities. Data in each set of observations were $\log 10(x + 1)$ transformed and subjected to analysis of variance using the SAS program. Means were classified according to the Bonferroni test at $P \leq 0.05$.

*Pathogenicity of P. neglectus to winter wheat:* This experiment, carried out in 1992, was located in the same field as described, and was part of a 3-year integrated management program (IMP) comparing six different rotational practices. In 1991, a maize crop had reduced *H. avenae* to a mean level of 25 ± 7.7 eggs/g soil; densities of *P. neglectus* in maize had been 89 ± 50.5/g roots at 72 days after sowing. Eight replicates of wheat line RE607, both resistant and tolerant to *H. avenae* (17), and 16 replicates of susceptible wheat cv. Arminda were grown in 6 × 10 m plots, treated or untreated with a mixture of carbofuran (4%) and isophenphos (2%) (1.2 kg a. i./ha), at sowing (12 November 1991). Population densities of nematodes and growth parameters were estimated at 1–2 leaves (Feekes scale 1) on 14 January 1992, and two nodes (Feekes scale 7) on 20 May 1992, by the methods previously described. At each sampling date, weights of foliage from two 0.20-$m^2$ (two rows × 0.5 m) areas were recorded after drying at 108 C for 24 hours. At harvest, plants were collected from six 0.20-$m^2$ (two rows × 0.50 m) areas in each plot. The ears were cut, threshed, and the grain weighed. Data were subjected to analysis of variance with the SAS program. Means were classified according to the Bonferroni test at $P \leq 0.05$.

## RESULTS

*Population dynamics of P. neglectus in the field:* In the experimental blocks, resistant oat cv. Panema consistently decreased *H. avenae* population densities, and when grown consecutively maintained them at a low density. In contrast, population densities increased and were maintained at a greater density when the susceptible cv. Peniarth was grown (Table 1). Following harvest in 1989, the low and moderately infested sites were clearly differentiated and were used for the subsequent experiments with wheat. The root densities of *P. neglectus* in both wheat cultivars cv. Fidel and cv. Arminda varied with *H. avenae* infection. *Pratylenchus* densities were lower ($P \leq 0.05$) where *H. avenae* infections were high, and higher where these were low (Table 2).

The seasonal population dynamics of the two nematodes were monitored in samples from consecutive crops of wheat cv. Arminda at low and moderate *H. avenae* initial infestations. The differential *H. avenae* population densities were perpetuated on the first wheat crop (Block C, 1991 and 1992; Table 1). In both years, root infections of *P. neglectus* were higher in plants grown at low *H. avenae* densities (Figs. 1A,B, Table 3). The numbers of *Pratylenchus* females and juveniles were different soon after germination in December 1990. The difference was maintained during winter and became more marked in March 1991. Thereafter, and while plants were tillering, the densities of *P. neglectus* decreased. But in June 1991, there were fewer ($P \leq 0.05$) *P. neglectus* eggs in roots moderately infected by *H. avenae* (Table 3). On the second wheat crop in January 1992, the difference between *Pratylenchus* population densities in the two *H. avenae* treatments was less than in 1991 (Fig. 1A). In later samples the difference became pronounced, and more vermiform stages were recovered from roots in low-density *H. avenae* treatments. The proportion of eggs in the *Pratylenchus* infections was lower in moderately infected *H. avenae*

TABLE 1. Population densities of *Heterodera avenae* and sequences of cereal cropping (1982–92) in a rotation designed to produce differential infestation densities of *H. avenae* for experiments in harvest years 1990 (Blocks A and B), 1991, and 1992 (Block C).

| | Block | | | | | |
|---|---|---|---|---|---|---|
| | A | | B | | C | |
| | Level of *H. avenae* infestation | | | | | |
| Harvest year | Low | Moderate | Low | Moderate | Low | Moderate |
| 1982 | Welam (R)† | Aramir (S) | Panema (R) | Peniarth (S) | Panema (R) | Peniarth (S) |
| 1983 | Panema (R) | Peniarth (S) | Panema (R) | Peniarth (S) | Wheat Talent (S) | |
| 1984 | Panema (R) | Peniarth (S) | Panema (R) | Peniarth (S) | Panema (R) | Peniarth (S) |
| | 0 | 10.2 (8.0)‡ | 0 | 65.5 (30.8) | 0.1 (0.1) | 61.7 (16.5) |
| 1985 | Panema (R) | Peniarth (S) | Wheat experiment | | Maize LG11 | |
| | 0.3 (0.5) | 20.2 (8.4) | | | 0 | 15.3 (3.8) |
| 1986 | Wheat experiment | | Panema (R) | Peniarth (S) | Panema (R) | Peniarth (S) |
| | | | 0.1 (0.1) | 15.5 (2.7) | 0.1 (0.1) | 6.2 (2.8) |
| 1987 | Peniarth (S) | Peniarth (S) | Wheat Fidel | | Panema (R) | Peniarth (S) |
| | | | 0.3 (0.3) | 13.5 (4.4) | 0 | 33.9 (8.7) |
| 1988 | Peniarth (S) | Peniarth (S) | Panema (R) | Peniarth (S) | Wheat Arminda | |
| | 0.7 (0.6) | 90.1 (20.8) | 0.2 (0.2) | 75.9 (16.1) | 0.4 (0.7) | 36.7 (15.5) |
| 1989 | Wheat Arminda | | Wheat Fidel | | Panema (R) | Peniarth (S) |
| | 5.5 (2.7) | 46.2 (9.8) | 0.1 (0.2) | 40.7 (7.7) | 0.7 (0.5) | 99.0 (37.8) |
| 1990 | Wheat Fidel | | Wheat Arminda | | Panema (R) | Peniarth (S) |
| | 12.7 (5.0) | 36.8 (4.7) | 0.8 (0.5) | 28.9 (7.3) | 0.3 (0.2) | 53.5 (12.0) |
| 1991 | | | | | Wheat Arminda | |
| | | | | | 11.7 (10.2) | 81.3 (18.7) |
| 1992 | | | | | Wheat Arminda | |

† *H. avenae* resistant (R) and susceptible (S) barley (cvs. Welam and Aramir) and oat (cvs. Panema and Peniarth).
‡ Eggs and juveniles per g soil in October, means (±SE) of five replicate samples.

roots from April through June 1992 (Table 3). In lightly infested plots, numbers of *H. avenae* J2 reached maxima of 5 and 30/g root in March 1991 and April 1992, respectively (Figure 1B). In moderately infested plots, these maxima were greater at 160 and 110 J2/g root in March 1991 and 1992. Sedentary stages of *H. avenae* were found in March to June 1991 (160 to 110/g root), in moderately infested plots only, and in both plots in smaller numbers in 1992 (10 to 35/g root).

*Reproduction of P. neglectus on oat cv. Panema and cv. Peniarth:* In a glasshouse pot experiment, there were no differences in the numbers of *P. neglectus* vermiform stages or eggs in the roots of the two oat cultivars after 72 days (Table 4).

*Split-root experiment:* In petri dishes in which both halves of the split-root systems were inoculated with *P. neglectus,* the nematode laid eggs, and numbers of vermiform stages increased during the 50-day experiment (Table 5). There was considerable variation between replicates. In split roots of plants inoculated with both nema-

TABLE 2. Population densities of *Pratylenchus neglectus* and *Heterodera avenae* (nematodes per g root) in two wheat cvs. Fidel and Arminda with moderate and low infections of *H. avenae,* at different stages of growth (Blocks A and B).

| Mean preplant *H. avenae* infestation (eggs + J2/g soil) | 1 node (3 May 1990) | | Flowering (8 June 1990) | |
|---|---|---|---|---|
| | *H. avenae* | *P. neglectus* | *H. avenae* | *P. neglectus* |
| 2.9 (3.49) | 8.4 (8.49) a† | 172.8 (106.28) a | 1.4 (1.19) a | 310.4 (62.97) a |
| 43.0 (9.08) | 66.9 (24.47) b | 74.6 (34.64) b | 28.1 (7.92) b | 81.5 (62.31) b |

† Means (±SE) of 10 replicate samples. At each growth stage, pairs of means within a column followed by the same letter were not significantly different at $P \leq 0.05$, by the Newman-Keuls test.

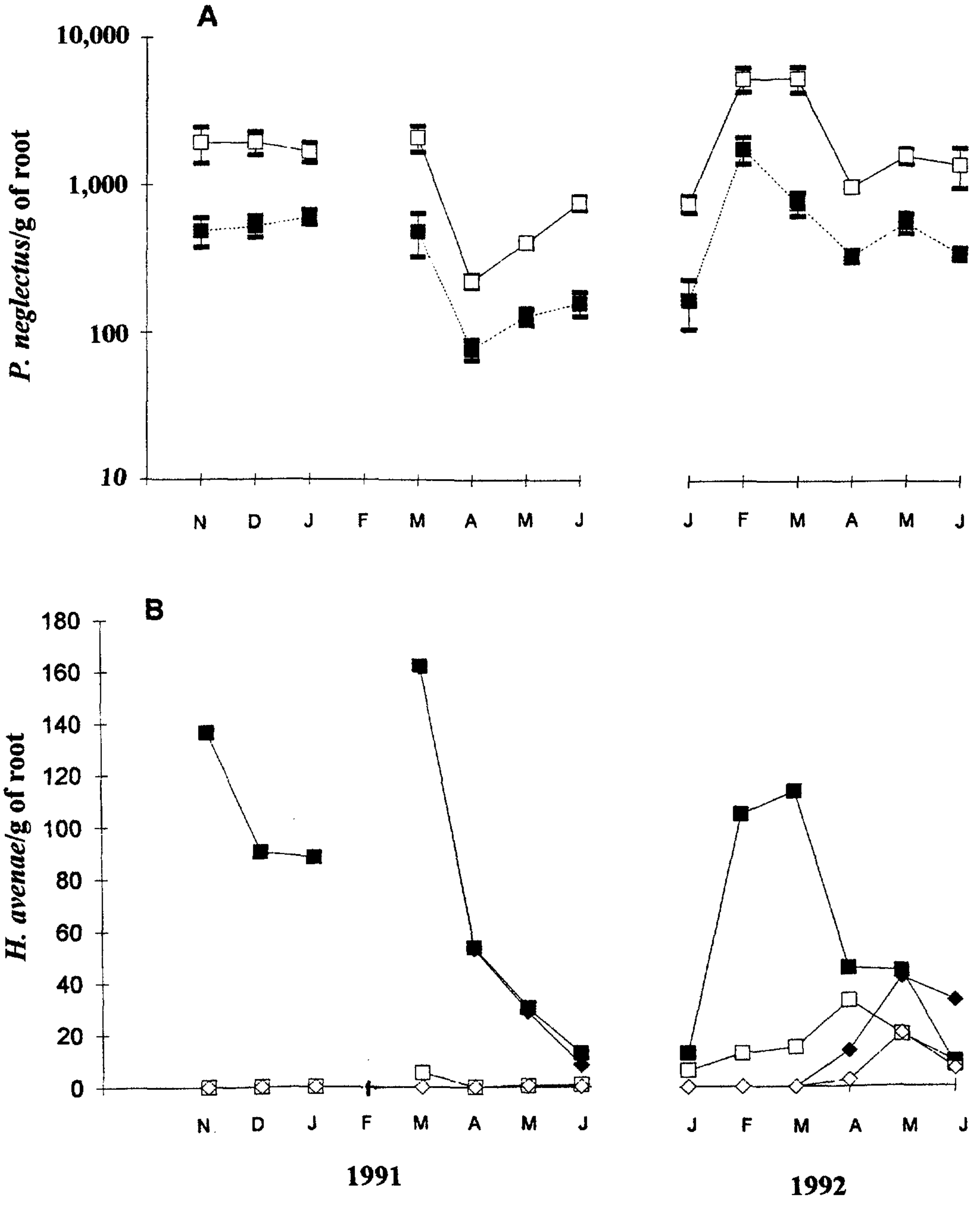

FIG. 1. Populations of *Pratylenchus neglectus* and *Heterodera avenae* in the roots of wheat cv. Arminda in two consecutive crops, 1991 and 1992. A) Mean and standard error of the mean of *P. neglectus* females and juveniles in plots lightly (□) or moderately (■) infested by *H. avenae*. B) *H. avenae* second-stage juveniles (□,■) and of later stages (◇,◆) in plots lightly (□,◇) and moderately (■,◆) infested by the nematode.

tode species, there were fewer *P. neglectus* vermiforms and eggs than in the preceding treatment; egg numbers and numbers of eggs plus vermiforms were both smaller ($P \leq 0.05$). In contrast, the development of cyst nematode females were the same regardless of the inoculum applied to the other half root system.

*Pathogenicity of P. neglectus:* Preplant application of carbofuran and isophenphos re-

TABLE 3. Proportion of the *Pratylenchus neglectus* population present as eggs in the roots of wheat cv. Arminda grown in field plots with low (Low) and moderate (Mod.) infestations of *Heterodera avenae* in 1991 and 1992 (Block C).

| Inoculum of *H. avenae* | *P. neglectus* population: % eggs | |
|---|---|---|
| | Low | Mod. |
| | 1991 | |
| December | 17.6 (5.80) a† | 3.1 (1.50) b |
| January | 46.7 (7.70) a | 46.0 (4.20) a |
| March | 25.0 (13.0) a | 25.3 (8.80) a |
| April | 40.3 (10.2) a | 30.0 (2.20) a |
| May | 49.4 (5.50) a | 35.8 (11.30) a |
| June | 41.2 (5.10) a | 6.8 (4.30) b |
| | 1992 | |
| January | 9.0 (4.90) a | 7.4 (7.40) a |
| February | 5.4 (2.60) a | 7.1 (3.00) a |
| March | 33.4 (3.00) a | 36.1 (5.20) a |
| April | 58.1 (12.60) a | 38.1 (9.70) b |
| May | 49.1 (2.60) a | 41.7 (8.00) b |
| June | 43.8 (19.40) a | 21.2 (2.50) b |

† Means from five replicate samples (10 from April to June 1992) for each month followed by the same letter were not significantly different at $P \leq 0.05$, by the Newman-Keuls test.

duced the root density of *P. neglectus* in cv. Arminda in January 1992 (Table 6). At the second assessment (20 May 1992), *Pratylenchus* densities did not differ significantly. *H. avenae* densities were not affected by nematicide treatment at either assessment but, in May, there were fewer females in the resistant line RE607 than in cv. Arminda.

Mean plant weights and grain yields were not affected ($P \leq 0.05$) by the preplant treatment, nor were they related to the initial nematode densities (Table 6). Grain yield of wheat line RE607, when not treated, was greater ($P \leq 0.05$) than that of cv. Arminda.

## DISCUSSION

These observations from farm fields and from a laboratory experiment provide evidence of an inverse relationship between *P. neglectus* and *H. avenae* on winter wheat. Such a relationship has been suggested previously on barley, based on population changes in field plots (3). Most studies that have emphasized the importance of interspecific competition between nematodes have been in glasshouse pot experiments at optimal temperatures and high initial nematode inocula (10). Our observations recognized an inverse relationship in the field despite variations in crops, seasons, and initial densities of both nematodes. Earlier observations in the three plots showed that *P. neglectus* populations were initially identical (Rivoal, unpubl.). The indications from the field that reproduction of *P. neglectus* was inhibited in the presence of *H. avenae* were supported to some extent by the experiment with split-root systems. In this case, the number of *Pratylenchus* vermiforms and eggs was 33% fewer on root systems when the other half was infected by *H. avenae* than when both halves were infected by *P. neglectus*.

In the field, the inhibition of *P. neglectus* on wheat was seen to extend throughout the long growing period of the host. Consequently, populations of the lesion nematode may have been controlled. In contrast, on *H. avenae*-resistant cultivars it is possible that loss of the inhibitory effect associated with cyst nematode development might lead to greater numbers of *Pratylenchus*. Prolonged use of such resistant cultivars might lead to the emergence

TABLE 4. Population densities of *Pratylenchus neglectus* in the roots of two oat cultivars differing in reaction to *Heterodera avenae* at 72 days after planting in soil infested with 1,652 ± 491 *P. neglectus*/100 g soil.

| Cultivar | Reaction to *H. avenae* | *P. neglectus*/g root | | |
|---|---|---|---|---|
| | | Females | Juveniles | Eggs |
| Panema | R† | 172.6‡ a | 855.3 a | 725.0 a |
| Peniarth | S | 257.1 a | 1,047.6 a | 878.4 a |

† R (resistant) or S (susceptible).
‡ Means of four replicates in a column were not significantly different at $P \leq 0.05$ by the Newman-Keuls test.

TABLE 5. Numbers of *Pratylenchus neglectus* (Pn) and *Heterodera avenae* (Ha) 50 days after single or combined inoculations of split-root systems of wheat cv. Arminda grown in petri plates.

| Inoculum | | | Nematodes/half-root system | | | |
|---|---|---|---|---|---|---|
| | | | *P. neglectus* | | | *H. avenae* |
| Half-root A | Half-root B | Replicates | Females + juveniles | Eggs | Vermiforms + eggs | J4 females + adult females |
| 24 Pn | 24 Pn | 25 | 50 ± 33.5† | 44 ± 26.5 | 94 ± 48.7 | |
| 24 Pn | 8 Ha | 16 | 36 ± 30.1 | 27 ± 23.1 | 63 ± 51.3 | 1.8 ± 1.51 |
| 8 Ha | 8 Ha | 10 | | | | 1.4 ± 1.00 |
| | | | ns‡ | * | * | ns |

† Means ± SE.

‡ Difference between means in a column is significant (*) or not significant (ns) at $P \leq 0.05$, by the Bonferroni test.

of other root parasites as damaging pests in intensive cereal production.

In the field, establishment of sedentary stages of the cyst nematode appeared to coincide with the relative reduction in *P. neglectus* infections. The split-root experiment may indicate that the effects of *H. avenae* on *P. neglectus* were indirectly mediated as the two species were confined to separate halves of the root system, thus preventing direct competition. The role of translocatable compounds, perhaps resulting from the establishment of syncytial feeding cells, has been suggested to be implicated in interactions between *Pratylenchus* and the sedentary endoparasite *M. incognita* on tomato and soybean (7,8).

Our attempt to evaluate the pathogenic-

TABLE 6. Populations of *Pratylenchus neglectus* and *Heterodera avenae* and growth and yield of wheat cv. Arminda and line RE607 at different growth stages in plots treated (T) or untreated (NT) with 1.2 kg a. i./ha of a mixture of carbofuran (4%) + isophenphos (2%) before planting in November 1991.

| | | *H. avenae* | | Shoot weight g/plant | Grain weight g/m$^2$ |
|---|---|---|---|---|---|
| | *P. neglectus*/g root | Total/g root | Females/g root | | |
| | | 1–2 leaves (14 January 1992) | | | |
| Arminda | | | | | |
| T | 86.9 a† | 3.2 a | — | 1.9 a | — |
| NT | 286.6 b | 16.9 a | — | 1.3 a | — |
| RE607 | | | | | |
| T | 185.0 ab | 3.6 a | — | 1.3 a | — |
| NT | 353.9 b | 13.8 a | — | 1.4 a | — |
| | | Two nodes (20 May 1992) | | | |
| Arminda | | | | | |
| T | 260.6 a | 76.2 a | 13.6 a | 95.4 a | — |
| NT | 470.9 a | 73.0 a | 15.1 a | 94.7 a | — |
| RE607 | | | | | |
| T | 313.6 a | 48.8 a | 0.2 b | 100.9 b | — |
| NT | 371.8 a | 34.0 a | 0.5 b | 113.6 b | — |
| | | Harvest (8 August 1992) | | | |
| Arminda | | | | | |
| T | — | — | — | — | 682.3 bc |
| NT | — | — | — | — | 663.5 c |
| RE607 | | | | | |
| T | — | — | — | — | 751.3 ab |
| NT | — | — | — | — | 767.9 a |

† Means, per date within a column, of eight and four replicates for Arminda and RE607 respectively, followed by the same letter are not significantly different at $P \leq 0.05$ by the Bonferroni test. Females + juveniles for *P. neglectus*.

ity of *P. neglectus* on winter wheat by application of the combination of carbofuran and isophenphos was unsuccessful, although the treatment reduced ($P \leqslant 0.05$) the infection in cv. Arminda, at the 1–2 leaf stage. The failure to demonstrate improved growth after *P. neglectus* control may have been because *P. neglectus* densities were below the damage threshold or because control was not effective for a long enough period. Other results (Lasserre and Rivoal, unpubl.) have shown that *P. neglectus* damages winter wheat when densities approach 3,000/g root, at the 1–2 leaf stage. This population density is an order of magnitude greater than in the present observations.

These studies sought to evaluate the consequences of long-term use of major gene resistance to control *H. avenae* on cereals. The field trials confirmed the effectiveness of winter oat cv. Panema for *H. avenae* control, but indicated a possible danger of increasing population densities of *P. neglectus*. Two successive nonhosts of cereal cyst nematode (corn Zea mays and resistant wheat) did not lead to damaging *Pratylenchus* densities. Nonetheless, other more prolific species might be damaging in similar circumstances (11). Managing cereal nematodes by alternating cyst nematode resistant and susceptible cultivars so as to also control lesion nematodes would certainly be more important in hotter, drier climates, which exacerbate damage caused by both cyst and lesion nematodes (21,23). Alternating cultivars resistant and susceptible to cyst nematodes also reduces selection pressure for the emergence of increased virulence within the population (24). Recently developed wheat lines with partial resistance may have a useful role in controlling *H. avenae* just below the damage threshold, while still inhibiting *Pratylenchus* reproduction (16). There are no reliable sources of *Pratylenchus* resistance in small grain cereals (22). If there is some form of induced suppression of *Pratylenchus* by cyst nematodes, further investigation might lead to an exploitable means of controlling these nematodes.

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