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Field response to *Pratylenchus thornei* of a wheat line with the *CreAet* gene for resistance to *Heterodera avenae*

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Abstract

The gene *CreAet* for resistance to *Heterodera avenae*, transferred from *Aegilops triuncialis* to *Triticum aestivum* introgression line TR-353, was assessed for responses to *Pratylenchus thornei* under field conditions. After 2.5 months, *P. thornei* infestation on TR-353 was similar to those on its progenitors (*T. aestivum* H10-15, *T. turgidum* H1-1 and *A. triuncialis* A-1) and on the cultivar Capa. After 5 months, TR-353 hosted significantly more *P. thornei* per plant than *A. triuncialis*, *T. aestivum* H10-15 or cultivar Rinconada, being very close to the maximum value obtained from *T. turgidum*. The final infestation of line TR-353 by *H. avenae* was significantly lower than on the other plants, except for *A. triuncialis*. In addition, at 2.5 months, the abundance of *P. thornei* on TR-353 was intermediate between the introgression wheat line H93-8 (*Cre2* gene) and the cultivar Loros (*Cre1* gene), but the final number of *P. thornei* per plant on TR-353 was significantly greater than on Loros. Line TR-353 was not able to control *P. thornei* in the field, but it confirmed its resistance to *H. avenae*, which was significantly lower than those due to *Cre1* and *Cre2* genes. No competition was observed between *P. thornei* and *H. avenae* populations on line TR-353 or *A. triuncialis*.

Introduction

Most of the damage caused by nematodes in cereal crops is due to *Heterodera avenae* and to the root-lesion nematodes, *Pratylenchus* spp., often both occurring together. *Pratylenchus thornei* is one of the most common species in wheat worldwide and is responsible for reduced wheat yields under arid conditions (Orion et al., 1984). In Spain, *Pratylenchus* spp. are representative of the cereal-leguminous rotations of the Central Region (Nombela et al., 1994), where *P. thornei* often supplants *H. avenae* as a major parasite of wheat (Tobar et al., 1995b). Integrated control of *P. thornei* including farm hygiene, crop rotation with poor host crops and use of tolerant and resistant wheat cultivars offers an effective alternative to uneconomic nematicides (Thompson et al., 1999). Wild cereal species, especially *Aegilops* spp. are considered to be the best source of resistance to *Pratylenchus* spp. and *H. avenae* (Thompson and Haak, 1997; Romero et al., 1998). To date, only the *Cre1* gene of resistance to *H. avenae* has been found in a cultivated wheat line (O'Brien et al., 1980) and several factors of resistance to this nematode (genes *Cre2* to *Cre6* and *CreAet*) have been transferred to hexaploid wheat from wild *Aegilops* spp. (Delibes et al., 1993; Eastwood et al., 1991, 1993; Jahier et al., 1996; Ogbonnaya et al., 2001; Romero et al., 1998). Recently, gene *CreAet* was termed *Cre7* (McIntosh et al., 2001). Unlike cereal cyst nematode, no wheat cultivars with resistance to *Pratylenchus* spp. are commercially available (Thompson et al., 1999; Nicol, 2001), although some differences among wheat lines or varieties in their resistance and/or tolerance to these nematodes have been reported (Farsi et al., 1995; Tobar et al., 1995a; Vanstone et al., 1998). The Australian bread wheat line GS50a, selected from Gatcher, is partially resistant, reducing considerably the reproduction rates of *P. hornei*, compared to some commercial wheat

cultivars (Thompson and Clewett, 1986). Recently, the Iraquian landrace AUS4930 was identified in Australia as simultaneously resistant against *P. thornei* and *H. avenae* in the field (Nicol et al., 1999). In previous work (Nombela and Romero, 1999), the *Cre2* gene, present in the wheat/*A. ventricosa* introgression line H93-8 and conferring resistance to *H. avenae* (Delibes et al., 1993), was evaluated for response to *P. thornei*, and we observed that neither line H93-8 nor its progenitors were resistant to *P. thornei* in the field.

This paper reports the response, under field conditions, of another wheat line, TR-353, bearer of the gene *CreAet* for resistance to *H. avenae* transferred from *A. triuncialis* (Romero et al., 1998), by means of a procedure similar to that previously used to transfer the gene *Cre2* to the line H93-8 from *A. ventricosa* (Delibes et al., 1993). The response of line TR-353 to *P. thornei* is compared, firstly, with the responses of its parentals and, secondly, with other plants carrying the genes *Cre1* and *Cre2* for resistance to *H. avenae*. In addition, a comparative study on the field resistance to *H. avenae* among these lines or cultivars was carried out, and the possible interactions between both nematode populations were evaluated.

Materials and methods

Plant material

The lines or cultivars used in this study were the introgression wheat line TR-353 (bearer of the gene *CreAet*), its progenitors *A. triuncialis* A-1, *T. turgidum* H1-1 and *T. aestivum* cv. Almatense H10-15, as well as *T. aestivum* cv. Loros and the introgression line H93-8 (bearing the genes *Cre1* and *Cre2*, respectively). The commercial varieties *T. aestivum* cvs Capa and Rinconada (both susceptible to *H. avenae*) were used as controls.

Experimental procedure

The assays were carried out at 'La Poveda' Experimental Station, close to Madrid (Spain), in a plot approximately 3.5 × 1 m. The soil was naturally infested with *H. avenae* (16 eggs + juveniles per 100 cm^3 soil) and *P. thornei* (88 nematodes per 100 cm^3 soil). The top layer of soil was homogenized before 30 individual pre-germinated seeds from each line or variety were transplanted into 30 buried plastic cylinders (11 cm diameter, 10 cm high) open at each end, following a complete block design. Two samplings were carried out at 2.5 and 5 months after sowing, respectively. The time period of 2.5 months for the first sampling (February) allowed *P. thornei* to complete its biological cycle under the environmental conditions of our experiment. At the time of the second sampling (April), plants had developed to ear emergence and *H. avenae* had completed its life cycle. Fifteen plants from every line or variety were collected in each sampling, and every individual plant was deposited into a plastic bag together with the soil in the corresponding cylinder.

Analysis of P. thornei *populations*

After each sampling, every plant was carefully separated from the soil in its cylinder and this soil was sieved and homogenized. Individuals of all ages of *P. thornei* were extracted from a 100 cm^3 soil subsample processed by a modification of the sugar centrifugation method (Nombela and Bello, 1983). Nematodes were also extracted from the roots of each plant, after washing, weighing, cutting into 1 cm pieces and placing them on Baermann funnels for a week. The average number of nematodes (mean ± SE) from 10 replicates was referred to as nematodes per gram of roots, nematodes per plant or nematodes per 100 cm^3 soil. Data were compared, after $\log(x + 1)$ transformation, by ANOVA followed by Fisher's protected least significant difference (LSD) *post hoc* test.

Evaluation of the resistance to H. avenae

At the second sampling (5 months after sowing), roots were carefully washed and weighed and mature females of *H. avenae* were counted directly under the light microscope, prior to *P. thornei* extraction which was performed as previously described. *H. avenae* females from 10 plants of every line or variety were averaged (mean ± SE) and referred to as nematodes per plant or nematodes per gram of root. Data were $\log(x + 1)$ transformed and compared by ANOVA followed by Fisher's protected LSD *post hoc* test. Pearson's simple linear correlation between the abundances of *H. avenae* and *P. thornei* was calculated (StatSoft, 1994).

Results

Analysis of P. thornei *populations*

No significant differences between wheat lines or varieties were found in the weight of the roots from

both 2.5 and 5 month samplings (data not presented). At 2.5 months after sowing, the mean numbers of *P. thornei* per plant and per gram of root in the line TR-353 were not significantly different from its parents or the control Capa, but they were greater than those on cv. Rinconada (Figure 1). The same relationship was observed at 5 months, regarding the abundance of *P. thornei* per gram of root (Figure 1B). Nevertheless, at that time, the line TR-353 hosted a significantly greater number of *P. thornei* per plant than *A. triuncialis* A-1, *T. aestivum* H10-15 and Rinconada, and very close to the maximum of *T. turgidum* H1-1 (Figure 1A).

The number of nematodes recovered from soil in the cylinders with TR-353 plants was significantly greater than that of *A. triuncialis* A-1 and *T. aestivum* H10-15 in the first sampling, but it was not different from any line or variety at the end of the experiment, with very low values from all tested plants (Figure 1C).

Results comparing line TR-353 (carrying the *CreAet* gene) with H93-8 and cv. Loros (bearer of genes *Cre2* and *Cre1*, respectively) are shown in Figure 2. From the first sampling, the averaged abundances of *P. thornei* per plant and per gram of root in TR-353 were intermediate between those in Loros (minimum) and H93-8. However, significant differences between TR-353 and Loros were detected in both the number of nematodes per gram of root and per 100 cm^3 soil (Figure 2B and C). On the contrary, at the end of the experiment (5 months), both numbers of *P. thornei* per plant (Figure 2A) and per gram of root (Figure 2B) were significantly greater in TR-353 than in Loros. Nevertheless, no significant difference was detected in the number of nematodes remaining in the soil at the end of the experiment (Figure 2C).

Evaluation of the resistance to H. avenae

Five months after showing, the mean number of *H. avenae* per plant in TR-353 was significantly greater than in *A. triuncialis* A-1 but similar to *T. aestivum* H10-15, and less than *T. turgidum*, Capa and Rinconada (Figure 3A). Similar data were observed in the number of *H. avenae* per gram of root, but, in this case, the mean value from TR-353 was significantly different from all other plants tested (Figure 3B). The number of *H. avenae* per plant in the line TR-353 was significantly greater than in H93-8 and Loros, with no differences between these latter two (Figure 3A). The number of *H. avenae* per gram of root in TR-353 was the greatest too, although the value from Loros was significantly lower than that in H93-8 (Figure 3B).

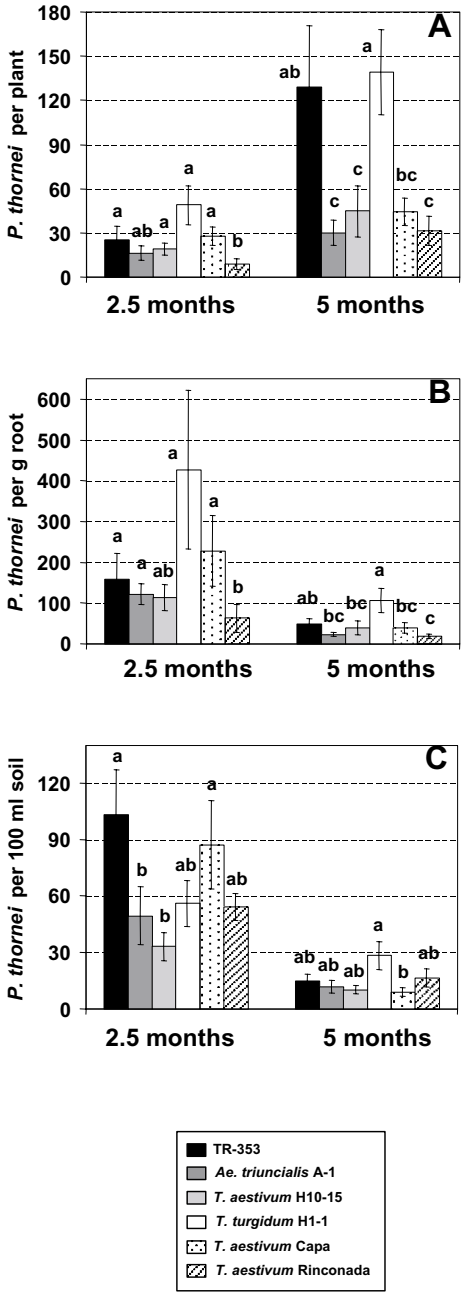

Figure 1. Evaluation of the susceptibility to *P. thornei* of the introgression wheat line TR-353, its progenitors (*A. triuncialis* A-1, *T. aestivum* H10-15 and *T. turgidum* H1-1) and the controls *T. aestivum* cvs Capa and Rinconada, at 2.5 and 5 months after sowing. Bars represent averaged numbers of nematodes on each line or variety. Thin lines represent the standard error of the mean. Means with the same letter in a sampling time do not differ significantly ($p < 0.05$) by Fisher's protected least significant difference test. (A) Number of *P. thornei* per plant. (B) Number of *P. thornei* per gram of root. (C) Number of *P. thornei* per 100 cm^3 of soil.

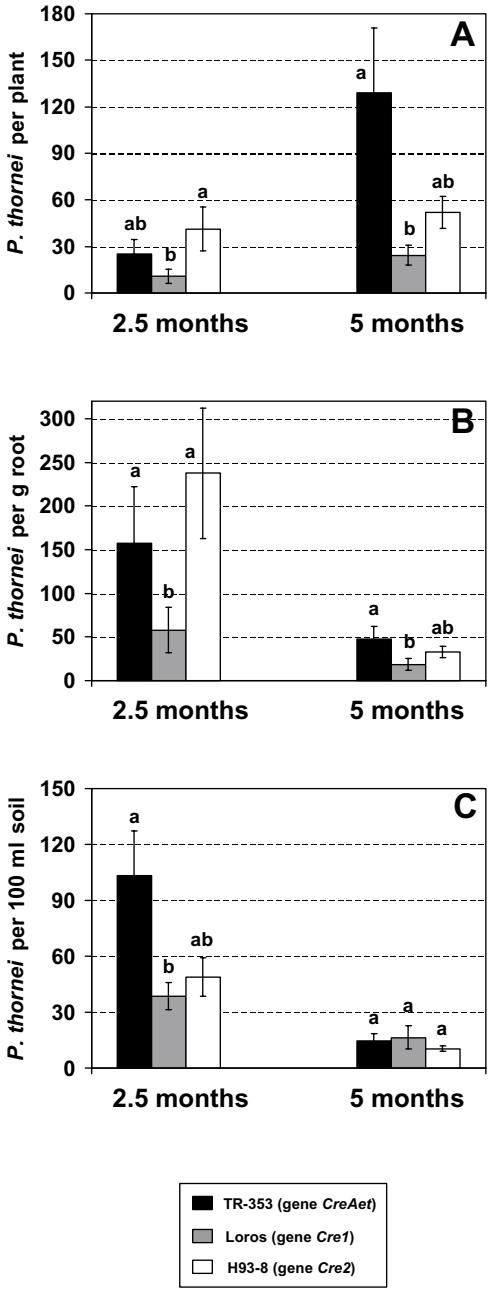

Figure 2. Evaluation of the susceptibility to *P. thornei* of the introgression wheat line TR-353, the introgression wheat line H93-8 and *T. aestivum* cv. Loros, at 2.5 and 5 months after sowing. Bars represent averaged numbers of nematodes on each line or variety. Thin lines represent the standard error of the mean. Means with the same letter in a sampling time do not differ significantly ($p < 0.05$) by Fisher's protected least significant difference test. (A) Number of *P. thornei* per plant. (B) Number of *P. thornei* per gram of root. (C) Number of *P. thornei* per 100 cm^3 of soil.

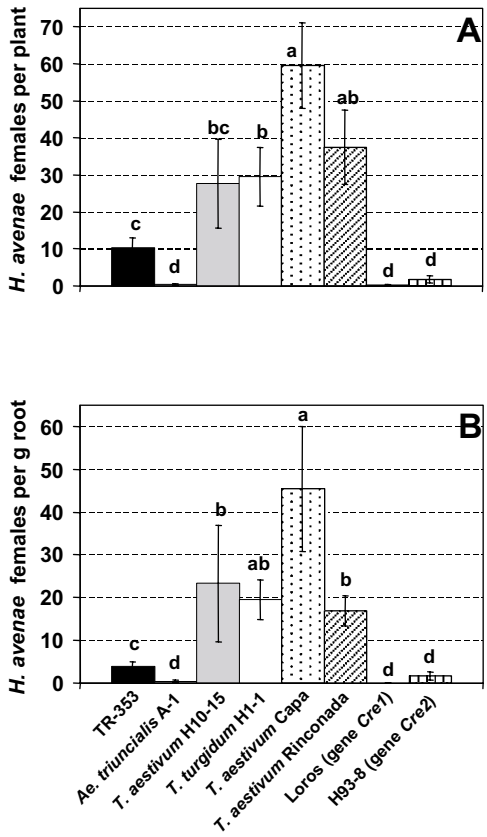

Figure 3. Comparison of the hosting capacity to *H. avenae* of the introgression line TR-353 with its progenitors (*A. triuncialis* A-1, *T. aestivum* H10-15 and *T. turgidum* H1-1), the controls *T. aestivum* cvs Capa and Rinconada, the introgression wheat line H93-8 and *T. aestivum* cv. Loros, at 5 months after sowing. Bars represent averaged numbers of nematodes on each line or variety. Thin lines represent the standard error of the mean. Means with the same letter do not differ significantly ($p < 0.05$) by Fisher's protected least significant difference test. (A) Number of *H. avenae* per plant. (B) Number of *H. avenae* per gram of root.

The correlation coefficients between the abundance of *P. thornei* and *H. avenae* on the line TR-353 and *A. triuncialis* at the end of the experiment were very low and not significant at $p < 0.05$ (data not shown).

Discussion

Comparison of line TR-353 with its progenitors

Both greenhouse and field assays are usually performed to test plants for resistance to *P. thornei* in wheat breeding programs. Field conditions are often

used in initial experiments and, subsequently, plants with a useful level of resistance are grown under controlled conditions (Thompson et al., 1999). Differences between results from natural and controlled conditions observed in a previous study on introgression wheat line H93-8 (Nombela and Romero, 1999) advised us to carry out this first attempt to test the host response to *P. thornei* of the new line TR-353 in the field. Plant resistance to *Pratylenchus* spp. in the field is frequently measured by counting the number of nematodes in soil samples at the start and/or end (after harvest) of the season (Rivoal et al., 1995; Nicol and Ortiz-Monasterio, 2001). Comparing soil populations of *P. thornei* has a limited usefulness when host plants are in the field, as the best information we usually get from this parameter is the penetration rate of the nematodes in the roots at sampling time. The low numbers of these nematodes obtained from soil at the final sampling cannot be misinterpreted in this case as a symptom of host resistance but that most of the nematodes were inside the roots at that time, with no big differences among the tested plants.

In our opinion, the best parameters to assess field resistance to *Pratylenchus* spp. are those measuring the nematode abundance in the roots. In the present study, the number of *P. thornei* both per plant and per gram of root were used, in accordance with other authors (Townshend, 1989; Farsi et al., 1995) to avoid restrictions from one or another method, as was discussed by Nombela and Romero (1999). At the end of the present study, line TR-353 was not resistant to *P. thornei* as it exhibited a level of susceptibility similar to or even greater than its progenitors (*A. triuncialis*, *T. aestivum* H10-15 and *T. turgidum*) and the cultivars Capa and Rinconada, the latter being the worst host for these nematodes. After 5 months, TR-353 hosted as many nematodes as *T. turgidum* which was clearly the most susceptible to *P. thornei* among the plants tested.

On the contrary, line TR-353 confirmed the results of Romero et al. (1998), controlling *H. avenae*, as it hosted less nematodes than its parentals *T. aestivum* H10-15 and *T. turgidum* or the controls Capa and Rinconada. At ear emergence time (5 months), only *A. triuncialis* had less *H. avenae* females than TR-353. In a similar way, we previously found that introgression line H93-8 hosted more *H. avenae* females than its donor *A. ventricosa* (Nombela and Romero, 1999). Apparently, genes regulating resistance to nematodes can display a lower level of expression when transferred to genotypes with higher ploidy levels (Bekal et al., 1998). This phenomenon has also been reported for other pathogens (Hanusova et al., 1996) and it can go from reduction of the gene expression (Chevre et al., 1989; Kerber and Dick, 1979) to complete suppression of resistance (Kerber, 1983).

Comparison of TR-353 with other lines bearing resistance genes

Line TR-353 was more susceptible in the field to *P. thornei* than the lines bearing other genes of resistance to *H. avenae*, especially *Cre1*. During the first 2.5 months of the experiment, line TR-353 hosted less *P. thornei* than line H93-8, although with no significant differences. This was due to a lower penetration rate of these nematodes in the roots of TR-353 plants, as was shown by the greater soil population. At the end of this study, line TR-353 was unable to control *P. thornei* population as it hosted more nematodes than line H93-8. The *Cre2* gene in the introgression line H93-8 was not able to control *P. thornei* under field conditions in our previous work (Nombela and Romero, 1999). Differences of TR-353 with Loros were even more dramatic, as cultivar Loros was one of the worst hosts for *P. thornei* (together with cv. Rinconada) in the present study.

Resistance to *H. avenae* observed in the line TR-353 was weaker than those conferred by two other known sources of resistance (*Cre1* and *Cre2*), although TR-353 was more resistant than H93-8 in a previous work (Romero et al., 1998). The most effective gene to control *H. avenae* was *Cre1*, followed by *Cre2*. The resistance gene *CreAet* as well as *Cre2* both act specifically on *H. avenae*. Inter- and intraspecific variability seems to be a common feature of genes conferring resistance to cereal cyst nematodes. It was demonstrated that resistance of wheat cv. Loros, regulated by the *Cre1* gene, did not apply to *H. filipjevi* and *H. latipons* nor to some *H. avenae* populations either (Bekal et al., 1998). Even the wheat line AUS4930, which is simultaneously resistant to *H. avenae* and *P. thornei* (Nicol et al., 1999), was ineffective to control *H. filipjevi* (Bekal et al., 1998). In addition to *CreAet* and *Cre2*, high specificity can be detected in other resistance genes transferred from wild Triticeae. So, genes *Cre3* and *Cre4*, incorporated into *T. aestivum* from *T. tauschii* (*A. squarrosa*), as well as both *Cre5* and *Cre6*, transferred from *A. ventricosa*, have shown different responses to several Australian and European *H. avenae* pathotypes (Rathjen et al., 1998; Ogbonnaya et al., 2001). Although, variability observed in other

work on the resistance efficiency of some *Aegilops geniculata* accessions seemed not to be related to the geographical origin of the cereal cyst nematode populations tested (Rivoal et al., 2000).

Interactions between P. thornei *and* H. avenae

An inverse relationship (interspecific competence) between *H. avenae* and *Pratylenchus* spp. was observed on wheat crops in field experiments (Lasserre et al., 1994; Rivoal et al., 1995). The same interaction had been previously suggested in barley (Cotten, 1970). However, no competition or any other relationship was detected between the population densities of *P. thornei* and *H. avenae* on the introgression wheat line TR-353 or its donor *A. triuncialis*. This was in accordance with our results previously obtained on the line H93-8 and its donor *A. ventricosa* (Nombela and Romero, 1999), where a negative correlation between the populations of both nematodes was detected only on *T. aestivum* cv. Loros. It has been postulated that *H. avenae* creates an unfavourable environment for *P. neglectus* and, consequently, cultivars resistant to cereal cyst nematodes favour the multiplication of root-lesion nematodes (Lasserre et al., 1994). Nevertheless, the final reason for the competition between both *H. avenae* and *Pratylenchus* spp., observed in some cultivars but not in others, remains unclear to date.

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