Impact of Soil Nematodes on Salt-marsh Plants: a Pilot Experiment

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ABSTRACT

DORMANN, C.F. and VAN DER WAL, R., 2001. Impact of Soil Nematodes on Salt-marsh Plants: a Pilot Experiment. *Journal of Coastal Research*, 17(2), 383–388. West Palm Beach (Florida), ISSN 0749-0208.

We tested whether the removal of nematodes by means of nematicide application changed plant performance or influenced plant competition. The study involved the two common plant species *Artemisia maritima* and *Festuca rubra* growing in intact sods collected from a temperate salt marsh. Half of the sods were treated with fenamiphos ('Nemacure', Bayer AG), a nematicide controlling both endo- and ectoparasitic nematodes. In untreated soil, the number of both total and plant-parasitic nematodes (7000 vs. 1000 per 100g fresh soil, respectively) was comparable to accounts from other salt marsh systems. After four months, the nematicide had reduced nematode numbers by 90%, but no influence on plant biomass or competitive ability of the two plant species was observed. As we did not follow the trajectory of nematicide effects on the nematodes, the exposure period of the test plants to low numbers of nematodes cannot be assessed. Experimental periods may need to be extended in order to evaluate long-term effects of reduced nematode numbers on plant productivity and plant competition in temperate salt marshes. On the basis of this pilot experiment we regard plant-parasitic nematodes to have a minor direct impact on productivity and interspecific relationship between the salt-marsh plant species investigated.

ADDITIONAL INDEX WORDS: *Artemisia maritima, fenamiphos, Festuca rubra, nematicide, plant competition, salt marsh.*

INTRODUCTION

The impact of belowground herbivores on plant species dynamics is poorly understood (BROWN, 1990, MORTIMER *et al.,* 1999). Most studies on herbivory focus on aboveground grazing, although the impact of belowground herbivores might be much greater (WEAVER and SMOLIK, 1987). Plants allocate as much as 60 to 90% of the primary production to belowground parts (STANTON, 1988), which are available to many soil-dwelling herbivores throughout the year.

Nematodes are the most abundant multicellular organisms in the soil (PETERSON, 1982a) and their impact on belowground processes is diverse. Nematodes can have a profound effect on nutrient cycling by feeding on bacteria (STANTON *et al.,* 1981, INGHAM *et al.,* 1986ab). Moreover, by grazing on arbuscular mycorrhizal fungi (AMF), fungal-feeding nematodes may reduce plant growth (INGHAM *et al.,* 1986b). Plant-feeding nematodes can affect plant performance directly or indirectly (VAN DER PUTTEN and VAN DER STOEL, 1998). In grassland ecosystems, where nematodes may consume as much as 60% of the total primary production (SMOLIK, 1977, ANDRZEJEWSKA and GYLLENBERG, 1980), nematodes have been considered the major herbivore (STANTON, 1988).

Plant-feeding nematodes may influence the competitive balance between plant species (GATES *et al.,* 1986; PRICE *et*

al., 1986). Such effects were observed in coastal foredune vegetation (VAN DER PUTTEN and PETERS, 1997), as well as in studies on crop-weed interactions (POWERS *et al.,* 1994; PANTONE, 1995), but in other agricultural studies, no such effects were found (CHEN *et al.,* 1995; PONCE *et al.,* 1995). The impact of phytophagous nematodes has only occasionally been studied in natural plant communities (DE ROOIJ-VAN DER GOES, 1995; STANTON, 1988; VAN DER PUTTEN and VAN DER STOEL, 1998) and direct evidence for impacts of plant parasitic nematodes on plant competition in natural plant communities is lacking (for indirect evidence see STANTON *et al.* 1981; INGHAM *et al.* 1986ab; VAN DER PUTTEN and PETERS, 1997).

On the basis of a series of pot experiments performed under greenhouse conditions, Van der Putten and colleagues showed that soil-borne diseases (plant-parasitic nematodes and pathogenic fungi) could play an important role in coastal foredune succession (VAN DER PUTTEN *et al.,* 1993; VAN DER PUTTEN and PETERS, 1997; VAN DER PUTTEN and VAN DER STOEL, 1998). There, *Ammophila arenaria* (L.) Link is followed in sequence by *Festuca rubra* ssp. *arenaria* L. and *Carex arenaria* L. together with *Elymus athericus* L. Biomass production in seedlings of all four plant species depended strongly on the origin of the rhizosphere soil, be it from early, mid or late successional foredune stages. When soils were treated by gamma radiation to destroy micro-organisms, differences between soil origins were no longer found. *Festuca* showed a

gradual decrease in biomass production along a series of unsterilised soils originating from *Ammophila* to *Elymus,* i.e. plants dominant earlier versus later in succession (VAN DER PUTTEN *et al.,* 1993). So far, there is still uncertainty on the role of plant parasitic nematodes in the functioning of disease complexes in foredune soils (VAN DER PUTTEN and VAN DER STOEL, 1998).

In the present study, we investigated the effects of nematodes on plant performance and plant competition in sods from a natural salt-marsh system. In line with the findings of Van der Putten and co-workers, soil organisms may be expected to influence plant performance in the higher parts of salt marsh, which are also dominated by *Festuca rubra* and *Elymus athericus* (OLFF *et al.,* 1997). Lower on the salt marsh, aboveground grazing by herbivores such as geese and hares strongly affects the rate of successional change (VAN DER WAL *et al.,* 2000b), plant species abundance (VAN WIJNEN *et al.,* 1999), and modifies competitive interactions among plants (DORMANN *et al.,* 2000, VAN DER WAL *et al.,* 2000a). The impact of belowground herbivores on vegetation processes, however, remain unclear.

We hypothesise that root-feeding nematodes may influence plant growth and, as a consequence, modify competitive interactions among plant species. As an initial test of this hypothesis, we applied nematicide to sods dominated by *Artemisia maritima* L., *Festuca rubra,* and mixtures of both. These plant species are characteristic of mid-elevational parts of temperate European salt marshes (WESTHOFF and DEN HELD, 1969).

METHODS

Site Description

The study was conducted on the island of Schiermonnikoog, the Netherlands. Sods were collected from a 40-year-old salt marsh in an area 45 cm above mean high tide, that is grazed by both geese and hares. *Artemisia* and *Festuca* together account for about 90% of total plant cover and grow in mixed and single-species stands, creating a fine-grained vegetation pattern. During vegetation succession, *Artemisia* and *Festuca* are inevitably replaced in older marshes by *Elymus athericus* (BAKKER *et al.,* 1997). We refer to OLFF *et al.* (1997) for a detailed description of the salt-marsh vegetation.

Sampling and Set-Up

On 20 June 1997, sods of 12 cm diameter and depth were cut out of pure and mixed stands of *Artemisia* and *Festuca,* and were fitted into same sized plastic pots. Other plant species occurring in the pots were picked out manually. Half of the pots were randomly assigned as controls, whereas the other half was treated with the slow-release nematicide 'Nemacure' (10 % Fenamiphos, Bayer AG, Germany), applied at the highest recommended dose of 20 g/m². To avoid negative impact on green plant parts, nematicide granules were manually pressed a few mm into the clayey soil surface (surface of controls pressed without granules). Nemacure specifically controls ectoparasites, endoparasites, free-living, cyst-forming and root-knot nematodes, but affects neither bacteria nor plants (Bayer AG, product information).

Each pot was assigned to one of three categories, *i.e. Artemisia* monoculture, *Festuca* monoculture, or mixed stand of the two species, and was either subject to the nematicide treatment or served as a control. For monocultures, we used 10 replicates per treatment, whereas 16 replicates were used for the mixed stands. Initial plant biomass was determined at the start of the experiment in 5 randomly selected additional sods of both monocultures and mixture. Labelled pots were placed randomly on a table outside in full daylight. Plants were watered during periods of drought. Transfer of nematodes via leaking water was prevented using dishes under every single pot. Pots were widely spaced to avoid direct contact or shading effects.

Pots were destructively sampled on 10 October 1997. Contents of all pots were washed over a sieve (mesh size 0.1 mm) and the plant material was separated into above- and belowground parts, dried at 70°C for 48 hours, and weighed. All aboveground biomass was alive, while dead roots and rhizomes not attached to live parts were discarded. These contributed less then 5% to belowground biomass. Soil samples of 3 randomly selected pots per treatment were used to determine nematode abundance and species composition.

Determination of Nematodes

For extraction of nematodes, 100g of fresh soil per pot (c. one third of the soil in the pot) was rinsed into an Oostenbrink III elutriator with a constant water pressure of 1 l/min (SOUTHEY, 1986). Nematodes in the water column were washed over 4 stacked sieves (each 0.045 mm mesh size), collected in a plastic bowl and poured onto a double-layer sandwich-filter made of cotton wool. The filters were kept overnight at 20°C in contact with water, allowing nematodes to move through the filter layer into the water. Nematodes from each pot were aggregated in 100 ml tap water and mixed thoroughly. Three subsamples of 2 or 5 ml (untreated and nematicide-treated, respectively) were inspected and counted under a stereomicroscope (32×). About hundred randomly selected nematodes per sample were determined to genus. The ratios of the abundance of the different genera were used to convert total number of counted nematodes into number per genus.

Statistics

Analysis of main effects employed analysis of variance (ANOVA); post-hoc comparisons were carried out using Tukey's honestly significant difference test (Tukey's hsd) for plant biomass, and least significant difference contrast (LSD) for nematode numbers. Transformed data met ANOVA assumptions of homoscedasticity and normal distribution.

RESULTS

Nematicide Application

At the end of the experiment, total number of nematodes was strongly reduced by nematicide application ($F_{1, 15} = 46.8$, $p < 0.001$; Figure 1). Reductions in number of nematodes were significant for all genera ($p < 0.05$); for the most com-
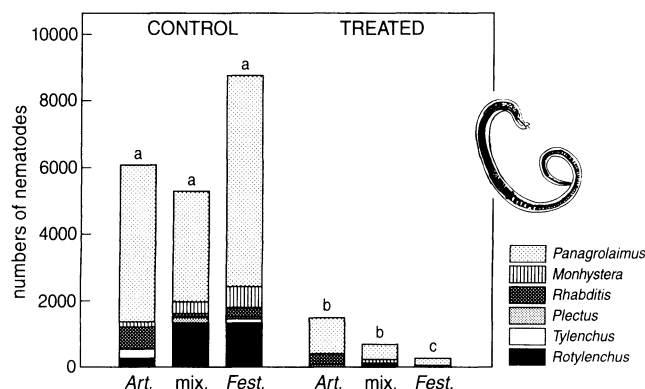
Fig. 1. Average number of nematodes per 100g wet soil of nematicide treated and control pots at the end of the experiment, indicated for the three different plant species compositions separately. Different letters indicate significant differences of total numbers according to LSD test (N = 3). Of the 6 genera found, only nematode species of the genus *Rotylenchus* are obligatory plant-parasitic. Nematodes of the genera *Monhystera*, *Panagrolaimus*, *Plectus*, and *Rhabditis* are bacteriophagous, while members of *Tylenchus* are fungivore to root-feeding nematodes. Art = *Artemisia*, Fest = *Festuca*, Mix is mixture of both.

Table 2. *Percentage* Artemisia *in competition pots of the two nematicide treatments.*

	Control[1]	Treated	F[2]	P
Aboveground	10.37 (1.12)	10.16 (1.64)	0.15	0.702
Belowground	9.83 (0.86)	8.72 (1.21)	0.88	0.354
Total	10.13 (0.76)	9.85 (1.32)	0.17	0.684

[1] Final percentage by weight ($\pm$ SE) of *Artemisia* in the mixture.
[2] F and P values derive from one-way ANOVA of arcsin(square-root)-transformed data. N = 16.

0.053). The density of *Rotylenchus* increased with an increase in belowground plant biomass (y = $52.86 \cdot e^{0.19x}$, $R^2 = 0.53$, $F_{1, 7}$ = 7.91, p < 0.05), regardless of plant species, which may explain part of the differences in numbers of *Rotylenchus* between *Artemisia* and *Festuca* or mixture soils. The number of nematodes of other genera did not differ significantly among plant species compositions (all with p > 0.4).

Plant Biomass

Effects of nematicide application on total plant biomass were negligible: Neither in pure *Artemisia* or *Festuca*, nor in mixed stands treatment effects were significant (nematicide application: $F_{1, 65} = 1.43$, p = 0.235). Moreover, when above- or belowground biomass was tested separately, no significant effects of nematicide treatment were found (Table 1). There were significant differences among *Festuca*, *Artemisia*, and mixture ($F_{2, 65} = 19.55$, p < 0.001; interaction: $F_{2, 65} = 0.01$, p = 0.989), with *Artemisia* pots having a lower total biomass. Root-biomass production within the experimental period ranged between 70% (*Artemisia*) and 400% (*Festuca*) of initial weight, supplying the plant-feeding nematodes with high amounts of young roots.

Root-total weight-ratios (RWR) of the treated *Festuca* pots were significantly lower than controls (Table 1), indicating a slight impact of nematodes on the allocation of biomass in the grass. *Artemisia* showed no such response, and also mixtures were seemingly unaffected by nematicide treatment.

The effects of nematodes on the competitive outcome between *Artemisia* and *Festuca* were assessed in pots comprising a mixture of both plant species. The percentage *Artemisia* of total biomass did not change with the application of nematicide (Table 2). Apparently, nematicide addition did not affect the competitive outcome between the two plant species.

monly observed genera *Panagrolaimus* and *Rotylenchus*, numbers were 88% and 95% lower, respectively.

Number of Nematodes in Untreated Pots

The total number of nematodes in untreated pots was c. 7000 individuals per 100g of fresh soil (Fig. 1). Most belonged to the genus *Panagrolaimus* (71%), opportunistic bacterial-feeders, common to terrestrial grassland systems. Second-most common were plant-parasitic nematodes of the genus *Rotylenchus*, with on average 1000 individuals per 100g (15%). The remaining genera were less abundant, all together comprising about 1000 ind. per 100g (14%). Of those, *Monhystera*, a bacterial-feeding nematode with several species in marine environments, was most abundant, followed by *Rhabditis*, *Tylenchus* and *Plectus*.

The density of nematodes in untreated pots did not differ among plant species compositions ($F_{2, 6} = 0.01$, p = 0.992). The average density of *Rotylenchus* in both *Festuca* and mixture pots was about 5× as high as in *Artemisia* pots, but differences were on the edge of significance ($F_{2, 6} = 4.97$, p =

Table 1. *Above- and belowground biomass (dry weight in g·m^{2} $\pm$ SE) and root-weight-ratios in the nematicide treatments.*

	Plant Part	N	Control	Treated	F[1]	P
Artemisia	aboveground	18	367.0 (34.5)	356.4 (129.1)	0.17	0.685
	belowground	18	901.2 (128.2)	989.6 (129.1)	0.44	0.515
	root-weight-ratio	18	0.725 (0.096)	0.696 (0.092)	0.46	0.507
Festuca	aboveground	19	485.5 (29.2)	459.0 (38.0)	0.42	0.526
	belowground	19	1170.9 (59.3)	1340.7 (118.5)	1.14	0.301
	root-weight-ratio	19	0.744 (0.044)	0.708 (0.029)	4.78	0.042
Mixture	aboveground	31	565.1 (26.5)	572.2 (25.6)	0.02	0.882
	belowground	31	1338.0 (77.8)	1491.0 (78.7)	1.86	0.183
	root-weight-ratio	31	0.720 (0.036)	0.699 (0.042)	2.41	0.131

[1] For above- and belowground biomass, F and P values derive from one-way ANOVA of $\log_{10}$-transformed data, for root-weight-ratios from arcsine-square root-transformed data. In a few pots plants died and were thus excluded from the analyses (*Artemisia* 2, *Festuca* 1, Mixture 1).

Interspecific competition had a much greater impact on the performance of *Artemisia* than had nematodes. While for both plant species no difference in biomass between nematicide application and control was detectable (Table 1), *Artemisia* biomass was reduced in the presence of *Festuca* in the mixtures. Compared with the monoculture, *Artemisia* pots experienced a biomass reduction of about 60% in the presence of *Festuca,* in nematicide-treated and control pots. On the other hand, no negative effects of interspecific competition on *Festuca* were measured.

DISCUSSION

In this study, we found no effect of applying nematicide on plant performance. Furthermore, no effect of nematicide on the outcome of plant competition could be established. At the end of the experiment, however, there was a substantial difference in numbers of plant-feeding nematodes between treated and untreated pots. We therefore conclude that belowground grazing by phytophagous nematodes (here only the genus *Rotylenchus*) does not seem to play a major role in salt-marsh areas dominated by *Festuca rubra* or *Artemisia maritima* as found on the island of Schiermonnikoog.

A number of studies emphasised the effects of nematodes on plant performance in semi-natural plant communities (STANTON, 1988; VAN DER PUTTEN and VAN DER STOEL, 1998; MORTIMER *et al.* 1999). Despite the impact of nematodes on plant performance, no effects on the outcome of plant competition were found in the experiments of which we are aware (CHEN *et al.,* 1995; PONCE *et al.,* 1995). In just a single study, leaf-feeding nematodes were shown to shift the competitive balance between plant species (PANTONE *et al.,* 1989, but see PANTONE, 1995).

The lack of a measurable effect in the present study of nematodes on plant performance can not be attributed to nematode densities. The total number of nematodes, as well as the number of plant-parasitic nematodes, was high, relative to other systems (*cf.* SOHLENIUS and SANDER, 1987). In the untreated salt-marsh soil, around $9 \cdot 10^6$ ind.$\cdot$m^{-2} were found, which is equivalent to a nematode biomass of nearly 1 000 mg per m^2 (conversion factor: 0.11 μg ind^{-1} SOHLENIUS and SANDER, 1987). On average, total nematode biomass in terrestrial ecosystems ranges between 120 and 450 mg$\cdot$m^{-2} (PETERSON, 1982b), which is less than half of our observations. Grasslands harbour, on average, more nematodes than any other terrestrial system, with 0.9 to $9 \cdot 10^6$ ind.$\cdot$m^{-2} as typical density in temperate regions (PETERSON, 1982a). This means that the density in our salt marsh ($\pm$ $9 \cdot 10^6$ ind.$\cdot$m^{-2}) is high even for grasslands. Recently, BONGERS *et al.* (1998) and BRINKMAN *et al.* (1998) reported from similarly high numbers of nematodes in two other salt marshes. Data from the lower end of a salt marsh in Georgia, USA, indicate a lower density, in the range of 1 to $6 \cdot 10^6$ ind.$\cdot$m^{-2} (TEAL and WIESER, 1966).

Several factors might have prevented the detection of nematodes affecting plant performance and plant competition. Although we used intact sods in the experiment, conditions might have differed from the situation in the field. Since we prevented soils from drying out, conditions might have been too benign to let the plants suffer from nematode grazing (*cf.*

MORTIMER *et al.,* 1999). In fact, the pronounced root growth we measured might be too fast to allow the nematodes to keep up with it: Root biomass is a pulsed resource, as fine roots are hardly available in winter, and increases faster than the generation time of its soil parasites. Nevertheless, belowground biomass in the experimental pots is not different from those measured in the field at the same site (VAN WIJNEN and BAKKER, 1999).

Another possible difficulty is the slow diffusion of the nematicide through the soil. The reduction of nematodes may therefore not have occurred until the end of the experiment. We did not assess when during the experimental period the differences emerged. It is also not sure whether the differences between control and nematicide-treated pots may have been due to reduction of nematodes or by prevention of reproduction and recruitment of the nematodes present at the start. By pressing the nematicide grains into the soil surface we tried to affect the upper soil layer, where most of the roots and, accordingly, plant parasitic nematodes were. Also, various studies have shown a high efficacy of the nematicide used already after two to four weeks (*e.g.,* BLACKBURN *et al.,* 1996; GREWAL *et al.,* 1997).

CONCLUSIONS

Measuring the impact of plant-feeding nematodes by means of chemical perturbation experiments is very much a "black-box approach," but may emphasise potential effects of nematodes on plants or plant competition outcome. Application of nematicide not only caused a difference in the number of plant-parasitic nematodes, but other groups of nematodes were also diminished. A decline in the number of litter-feeding nematodes may result in less nitrogen available to plants due to a decreased decomposition rate (ALKEMADE *et al.,* 1993), with suppressed plant growth as a consequence. Also, by diminishing the number of bacteria-feeding nematodes, nutrient turn-over can be suppressed (YEATES and COLEMAN, 1982, STANTON, 1988), thereby outbalancing the positive effect of reduced grazing by plant-parasitic nematodes. The studies conducted by INGHAM *et al.* (1985, 1986a,b) and STANTON *et al.* (1981), in which biocides were applied in an attempt to remove certain groups of belowground organisms from the soil community, indicated the opposite: plant shoot biomass as well as shoot nitrogen content increased when nematicides were applied.

These type of perturbation experiments therefore can only be the start of more detailed studies, dealing with groups of species, i.e. inoculated into sterile ground (see VAN DER PUTTEN and VAN DER STOEL, 1998). Furthermore, these experiments should also be performed in the field, and not only with potted soils from the field, and the time span should be adapted to the speed of the processes under study, which, in case of plant competition, is one or more years, instead of several months.

Despite the shortcomings of the study, we regard it to be unlikely that our findings can be explained by a series of counteracting knock-on effects, without detectable consequences for plants and their interactions. We demonstrated that nematode numbers in salt marsh soils can be success-

fully reduced by nematicide application. This opens an avenue to subsequent studies on the role of plant-parasitic nematodes in salt-marsh vegetation dominated by *Artemisia maritima* and *Festuca rubra*.

ACKNOWLEDGEMENTS

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