Ecology of the plant-feeding nematode fauna associated with sea buckthorn (*Hippophaë rhamnoides* L. ssp. *rhamnoides*) in different stages of dune succession

Frans C. Zoon * +, Sep R. Troelstra * and Paul W. Th. Maas +

* *Institute for Ecological Research, P.O. Box 40, 6666 ZG Heteren, The Netherlands,*
and + *Research Institute for Plant Protection (IPO-DLO), P.O. Box 9060, 6709 GW Wageningen, The Netherlands.*

Summary – A field survey was carried out to investigate the development of the plant parasitic nematode fauna under *Hippophaë rhamnoides* ssp. *rhamnoides* from the colonization to the degeneration stage. Samples from different sand dune locations along the Dutch coast were analysed and the occurrence and densities of different nematode taxa were studied in relation to soil parameters and plant productivity, using ordination and regression techniques. There appeared to be a succession of nematode taxa along with the development of soil and vegetation. The maturity index of the obligate plant-feeding nematode fauna and the mean number of species increased significantly. The characteristics of sites, with respect to soil parameters and nematode fauna, diverged as it reached the degeneration stage. *Tylenchorhynchus microphasmis* Loof and *Mesocriconema xenoplax* (Raski) were common in all stages. The abundance of plant feeding nematodes in the rhizosphere of *Hippophaë* increased towards later stages in a succession gradient, whereas population densities in the bulk soil remained practically constant. The status of *H. rhamnoides* as a host of several free-living plant-feeding nematodes is discussed.

Résumé – *Écologie de la faune nématologique phytoparasite associée à l'argousier* (Hippohaë rhamnoides L. ssp. rhamnoides) *pendant les états successifs des dunes maritimes sableuses* – Des échantillons de sol, prélevés dans plusieurs régions des dunes sableuses maritimes des Pays-Bas, ont été analysés en vue d'étudier les différents stades du développement de la faune nématologique phytoparasite depuis la phase de la colonisation jusqu'à celle de la dégénerescence d'*Hippophaë rhamnoides*. La présence et l'abondance des taxa ont été étudiées en fonction des facteurs physico-chimiques et biotiques du sol et de la vitalité d'*Hippophaë*. Une succession de taxa de nématodes se développe, en concordance avec la modification du sol et de la végétation. En conséquence, l'indice de maturité de la nématofaune phytoparasite obligée, ainsi que le nombre des taxa, augmentent de manière significative. Les caractéristiques des sites, en regard des facteurs édaphiques et de la nématofaune, montrent une divergence lors du stade de dégénerescence d'*Hippophaë*. *Tylenchorhynchus microphasmis* Loof et *Mesocriconema xenoplax* (Raski) sont présents et nombreux à tous les stades. Une étude plus détaillée montre que la densité des nématodes dans la rhizosphère d'*Hippophaë* augmente lors des stades tardifs, alors qu'elle reste pratiquement constante dans le « bulk-soil ». L'aptitude de *H. rhamnoides* en tant que plante-hôte de plusieurs nématodes ectoparasites est discutée.

Key-words : Nematodes, ecology, soil development, natural vegetations, herbivory, ordination.

Hippophaë rhamnoides L. ssp. *rhamnoides* is a pioneer shrub species on calcareous coastal sand dunes in north-western Europe (Pearson & Rogers, 1967). The dunes under *H. rhamnoides* vary in age from a decade to several centuries. Changes in the vegetation occur, although *Hippophaë* may remain the dominant species over a long period (van der Maarel *et al.*, 1985).

Different aspects of chemical and physical development of calcareous dune soils have been known for a long time (Salisbury, 1922; Olson 1958; Willis *et al.*, 1959) and were suggested to play a major role in the succession of vegetation. The main processes of development in calcareous dune soils are : *i)* accumulation of organic nitrogen, especially from symbiotic N_2-fixation by the actinomycete *Frankia* sp. in *Hippophaë* root nodules (Akkermans, 1971; Stewart & Pearson, 1967) and atmospheric deposition; *ii)* leaching of calcium and other cations (Salisbury, 1922; Stuyfzand, 1984; Rozema *et al.*, 1985); and *iii)* decreasing wind impact on locations behind a progressing coast line, leading to decreasing salt spray and a smaller particle size median of the sand.

The development of the nematofauna of dune soils has received little attention (Kisiel, 1970; Wasilewska, 1970, 1971). Nematofaunal changes in the calcareous sand dunes of Western Europe have hardly ever been studied. The colonization of young dunes by nematodes may depend on the rate of dispersal and reproduction, and on the availability of suitable niches. Presumably, some nematode species have a high dispersal rate or a broad ecological amplitude, whereas others are only slowly dispersed or have a relatively high degree of niche specialization. The stage of edaphic and vegetational

development may determine habitat suitability for different nematode taxa.

Plant-feeding nematodes were suggested as a cause of the decline of *H. rhamnoides* (Oremus, 1982; Maas *et al.,* 1983). Especially, the occurrence of *Longidorus* n. sp. (*L. dunensis* Brinkman *et al.*, 1987) in the late successional stage was considered to be important. Inoculation of a mixture of *L. dunensis* and *Tylenchorhynchus microphasmis* Loof in a pot experiment caused severe growth reduction of *H. rhamnoides* (Maas *et al.*, 1983). It was not clear, however, if these nematode species and their effects on plant vigour are of more than local importance, in other regions other species may be involved.

The results of a field survey on the occurrence of plant-feeding nematode taxa in different stages of *Hippophaë* succession are presented in this paper. An attempt was made to relate the presence and the density of nematode taxa to soil parameters and the productivity of the vegetation. Soil samples from vegetations preceding and succeeding those with *Hippophaë* were analysed in a study of a transect from young to old dunes. Furthermore, the nematode fauna of *Hippophaë* rhizosphere samples from different successional stages was analysed and compared to samples of the bulk soil to evaluate the importance of *Hippophaë* roots in the distribution of nematode taxa.

Table 1. Topography and some environmental parameters of sampling locations in the field survey.

Site nr.	Region	Coordinates NW/EL	Stage ([1])	pH	N ([2])	OM/N ([3])	NOD ([4])	VI ([5])
1	Texel I.	53° 08'/4° 47'	D	8.3	20.2	17.8	5	2
2	id.	53° 08'/4° 47'	So	8.2	23.4	18.8	1	4.5
3	Texel II.	53° 00'/4° 45'	P	7.9	10.8	19.4	9	5
4	id.	53° 01'/4° 44'	D	5.8	21.0	19.0	2	1.5
5	id.	53° 01'/4° 44'	Sb	7.6	17.0	19.4	0	5
6	id.	53° 01'/4° 44'	D	6.9	22.2	22.1	8	1
7	Castricum	52° 33'/4° 38'	D	8.2	35.1	18.8	40	1.5
8	id.	52° 33'/4° 38'	Ss	8.0	44.8	22.1	11	4.5
9	id.	52° 30'/4° 36'	So	8.2	39.3	21.6	4	5
10	id.	52° 32'/4° 36'	D	8.3	23.1	22.9	14	2
11	Oostvoorne	51° 55'/4° 03'	P	8.6	13.0	13.1	3	5
12	id.	51° 54'/4° 04'	D	8.4	28.5	14.4	0	2
13	id.	51° 54'/4° 04'	D	8.5	22.8	16.7	1	2
14	id.	51° 54'/4° 03'	D	8.5	23.6	18.6	7	1.5
15	id.	51° 55'/4° 04'	P	8.7	16.3	16.6	3	4.5
16	Schouwen I.	51° 44'/3° 43'	D	5.6	25.8	22.1	0	1
17	id.	51° 44'/3° 43'	Sd	8.2	18.6	20.4	0	4
18	id.	51° 44'/3° 43'	Sd	8.5	14.4	20.8	1	2
19	id.	51° 42'/3° 41'	P	8.4	17.8	23.6	2	2
20	id.	51° 42'/3° 41'	P	8.6	12.2	23.0	3	3.5
21	Schouwen II.	51° 42'/3° 44'	D	5.2	32.0	24.4	3	2
22	id.	51° 42'/3° 43'	So	5.7	14.9	22.8	3	4
23	id.	51° 42'/3° 43'	S	5.5	16.0	13.8	3	1

([1]) P : Early primary succession, < 20 years of *H. rhamnoides*.
   S : Early secondary succession after disturbance (o = overblown, b = blowout, d = digging activities, s = sludge deposit).
   D : Degeneration on stable sites, >> 20 years *H. rhamnoides*.
([2]) Total N mg/ 100 g.
([3]) Org. matter/N (w/w).
([4]) *Frankia*-nodules per seedling in pot bioassay.
([5]) visual *Hippophaë* vigour : 0 = dead, 5 = vigorous.

Methods

FIELD SURVEY

Sampling locations

Twenty-three scrubs were selected in six different dune areas (Table 1) which were at the most 160 kilometer apart. Within each area both vigorous and degenerating *Hippophaë* vegetations were sampled in mid September 1985. The oldest shoots (ramets) in the selected scrubs were between 15 and 20 years old. The sites were classified into three successional stages on the basis of studies on the geomorphological and vegetation history of the area and its present vegetation :

1. sites of early primary succession with a first vegetation of *H. rhamnoides*.

2. sites of early secondary succession, which had a regenerated (but not always vigorous) *Hippophaë* vegetation after soil disturbance either by wind or by digging; these sites were surrounded by non-disturbed vegetation which had developed much further (*e.g.* with *Rosa pimpinellifolia* L. or deciduous forest).

3. late successional stages with degenerating scrubs on soil which had remained *in situ* for at least a few decades after primary or (more often) secondary colonization. These sites had mixed scrubs or a sparse *Hippophaë* vegetation with an undergrowth of grass or moss.

Twenty soil cores (diam. : 2.5 cm) were taken from each site (about 20 m²) and divided into the 0-10 and 10-70 cm layers. The cores of each layer were carefully mixed together to form one sample per layer per site.

Plant parameters

The vigour of *Hippophaë* was estimated with an index for the visual shrub vigour (VI) (0 = dead, 5 = vigorous), which is significantly correlated with the mean biomass of current twigs and the xylem increment of one-year-old branches (Zoon, unpubl.). The percentage of fine root length of *Hippophaë* from the 10-70 cm soil samples infected with vesicular-arbuscular mycorrhiza (MYC) was assessed using the line-intersection method after staining with Chlorazole Black E. (Brundrett *et al.*, 1984). The *Frankia*-nodulation potential (NOD) was estimated by counting the number of nodules formed after 10 weeks on *Hippophaë* seedlings planted in 500 ml of the 10-70 cm soil sample from each site.

Soil chemical and textural analysis

Soil samples from each of the two layers were analysed to determine soil chemical and textural parameters. After drying (35 °C) and sieving (2 mm), soil samples were mechanically subdivided and part of each sample was ground in a mortar mill.

The pH was measured potentiometrically in 1:2.5 (w/v) suspensions in H_2O. Total P and total N were measured colorimetrically in single soil digests (Novozamsky *et al.*, 1984). The percentage organic matter (OM)

was estimated from the weight loss on ignition at 430 °C for 24 h. Percentage carbonates (mainly $CaCO_3$; LIME) was determined gas-volumetrically by treating samples with 4 M HCl. Exchangeable cations (Mg, K and Na) were determined by atomic absorption spectrophotometry after shaking soils with neutral ammonium acetate. Electrical conductivity (EC) was measured in 1:5 (w/v) suspensions in H_2O.

The soil texture was analysed by dry sieving (fractions > 53 μm), and a pipette method (fractions < 53 μm). The particle size median (PSM) and the percentage clay < 2 μm) were taken as characteristic parameters.

Ratios P/N and OM/N were calculated. The latter was assumed to reflect the C/N ratio, which itself was not determined.

Nematode fauna

Analysis of the nematode fauna was done only for the 10-70 cm layer, because roots of *H. rhamnoides* are present mainly in this layer (Oremus, 1982). Nematodes were extracted from a 500 ml subsample of the 20 mixed samples of a 20 m² plot by using the Oostenbrink elutriation method (Oostenbrink, 1960). The top sieve on the funnel was 2.5 mm mesh to improve the recovery of large nematodes. The funnel was emptied over sieves of 180 μm (2 ×) and 45 μm (3 ×) mesh, respectively. The fraction larger than 180 μm was extracted overnight through a 120 μm mesh gauze, the smaller sized fraction through a double cotton-wool filter.

Plant-feeding nematodes were counted at genus or species level. A few specimen from each taxonomic group in a sample were fixed and mounted for species identification. For Tylenchida the classification by Siddiqi (1986) was followed, except for the genera *Macroposthonia* and *Dolichorhynchus*, which have been synonymized with *Mesocriconema* (Loof & De Grisse, 1989) and *Tylenchorhynchus* (Fortuner & Luc, 1987), respectively. The successional position of each taxon was characterised by its optimum on the imaginary succession gradient (stage 1 to 3). These successional optima (SOPs) take into account both the frequency of occurrence and the population density and were calculated as follows :

$$SOP = 0.5 * \sum_{i=1}^{3} (Fi * i) / \sum_{i=1}^{3} (Fi) + 0.5 * \sum_{i=1}^{3} (Ni * i) / \sum_{i=1}^{3} (Ni)$$

Where *Fi* is the frequency of occurrence (positive/total samples) in stage *i*, and *Ni* the mean number per 500 ml soil calculated for the samples in stage *i* where the taxon occurred. In addition, the " matury index " of the plant-feeding nematofauna was calculated for each sample following Bongers (1990) as the weighted mean of the " maturity values " (1-5) of each individual present.

Statistical analysis

Simple correlations within and between environmental and nematode parameters were calculated. Canonical

Correspondence Analysis (CCA) (Ter Braak, 1987*a, b*) was used for analysis of the (unimodal) relations between nematode fauna and environmental parameters. The nematode data used were percentages of total plant-feeding nematodes. To obtain a small set of principal factors, the number of environmental parameters in the ordination was reduced by stepwise elimination of parameters which were correlated to others, or which were not correlated to the first four ordination axes. Significance of the eigenvalues of the first canonical axis and of the sum of the eigenvalues of all axes (trace) was tested by a Monte Carlo test with 99 random permutations of environment and nematofauna. For comparison, the data were also analysed by Redundance Analysis (RA), the linear analogue of CCA, and the use in CCA of nematode numbers instead of percentages was evaluated.

TRANSECT SAMPLING

Another series of samples was taken in September 1987 on a transect from beach to inner dunes on the former isle of Schouwen. A description of the sites, which represent successive vegetation types, is given in Table 2. Methods were the same as in the field survey, but now samples were collected from the 0 to 50 cm layer.

Table 2. Description of locations on the succession transect at Schouwen (coordinates as sites 16-18 in Table 1.).

Site	Distance to sea (m)	Dune type	Dominant vegetation
A.	200	embryo dune	*Elymus arenarius*
B.	500	low foredune	*Ammophila arenaria*
C.	530	id.	*H. rhamnoides* invading
D.	1160	flat inner dune	*H. rhamnoides* + meadow
E.	1220	id.	*Ligustrum vulgaris*

RHIZOSPHERE SAMPLING

In order to find out to what extent nematodes concentrate in the rhizosphere of *H. rhamnoides* four-month-old seedlings were planted in May 1987 near sites 11 and 12 of the field survey. In September the plants were dug up carefully and – with the adhering soil – taken into the laboratory. Samples of bulk soil from the 0 to 25 cm layer (approximately seedling rhizosphere depth) were collected at the same time, at a few dm from the seedling roots. The amount of " rhizosphere " soil attached to the roots was determined by subtracting the fresh weight

of the roots from the total weight of roots plus soil. Nematodes were extracted and counted as described above.

Results

FIELD SURVEY

Plant-feeding nematode fauna

Mesocriconema xenoplax (Raski, 1952), *Tylenchorhynchus microphasmis* Loof, 1960 and Tylenchidae were the most common taxa under *Hippophaë*. Less common or less numerous were *Rotylenchus goodeyi* Loof & Oostenbrink, 1958, *Paratylenchus* spp., *Meloidogyne* spp. (mainly *M. hapla* Chitwood, 1949 and *M. maritima* Jepson, 1987), *Helicotylenchus pseudorobustus* (Steiner, 1914) and *Pratylenchus* spp. [mainly *P. crenatus* Loof, 1960 and *P. penetrans* (Cobb, 1917)]. Some other taxa seemed to be restricted to certain regions. This was most clearly the case for *Longidorus dunensis* Brinkman *et al.*, 1987 and for *Geocenamus arcticus* (Mulvey, 1969) *, which were not present in samples from the isle of Texel and the area Schouwen II. *Paratrichodorus* spp. *P. pachydermus* (Seinhorst, 1954), *P. nanus* (Allen, 1957) and *P. teres* (Hooper, 1962), in descending order of importance) and *Bitylenchus dubius* (Bütschli, 1873) were absent from the Texel samples. *Rotylenchus robustus* (de Man, 1876) was found at only one site, possibly introduced by nearby agricultural activities. Other " minor " taxa in this survey were Heteroderinae (J2), *Telotylenchus ventralis* Loof, 1963, *Criconema annuliferum* (de Man, 1921) and *C. princeps* (Andrássy, 1962), *Criconemoides informis* (Micoletzky, 1922) and *C. amorphus* De Grisse, 1967, and *Hemicycliophora conida* Thorne, 1955.

The successional optimum points (SOPs) of *R. goodeyi, Paratylenchus, M. xenoplax* and *T. microphasmis* were between stage 1 and 2 (Table 3), whereas those of other taxa were between stage 2 and 3. *G. arcticus* and *H. conida* were found only in the degeneration stage (Table 3).

For taxa that were present in different stages of succession the coefficients of variation of the population density (as can be calculated from Table 3) generally increased in the later stages (*e.g. R. goodeyi* from 0.50 to 1.27). Only *T. microphasmis* and *M. xenoplax* showed decreased coefficients of variance in later stages (from 0.76 to 0.48 and from 1.30 to 0.92, respectively).

The number of taxa per sample ranged from 4 (sites 18 and 23) to 14 (site 14). The mean was higher in the

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* First record in the Netherlands.

Table 3. Frequency of occurrence and mean densities of plant-feeding nematodes as related to the stage of succession of *H. rhamnoides* vegetations. F = number of sites where taxon is present, N = mean number per 500 ml soil (mean of positive sites), SE = standard error of the mean, SOP = weighted optimum on succession scale 1-3. Different letters within the same line in the lower part of the table indicate significant differences ($p < 0.05$) in pairwise analyses of variance.

Stage of succession	1. Early primary (n = 5)			2. Early secondary (n = 8)			3. Late degeneration (n = 10)			
Nematode taxon	(F)	N	SE	(F)	N	SE	(F)	N	SE	SOP
Rotylenchus goodeyi	(3)	118	34	(4)	28	12	(4)	11	7	1.6
Paratylenchus spp.	(5)	9	4	(4)	5	2	(7)	6	2	1.9
Mesocriconema xenoplax	(5)	86	50	(8)	57	29	(10)	41	12	1.9
Tylenchorhynchus microphasmis	(4)	174	66	(7)	115	27	(10)	105	16	2.0
Rotylenchus robustus	(0)			(1)	20	20	(0)			2.0
Heteroderinae	(2)	1	0	(3)	5	4	(3)	2	0	2.0
Meloidogyne spp.	(3)	2	1	(2)	17	11	(7)	5	2	2.1
Tylenchidae	(5)	42	13	(8)	41	15	(10)	72	12	2.1
Telotylenchus ventralis	(1)	2	2	(1)	1	1	(2)	4	2	2.1
Pratylenchus spp.	(3)	7	3	(5)	38	15	(8)	25	11	2.2
Bitylenchus dubius	(1)	1	1	(1)	5	5	(3)	16	12	2.4
Criconema spp.	(0)			(1)	5	5	(1)	5	5	2.5
Paratrichodorus spp.	(1)	4	4	(4)	8	2	(6)	38	30	2.5
Helicotylenchus pseudorobustus	(1)	1	1	(3)	10	7	(7)	79	47	2.6
Criconemoides spp.	(0)			(1)	5	5	(4)	8	3	2.7
Longidorus dunensis	(0)			(2)	5	1	(5)	32	13	2.8
Geocenamus arcticus	(0)			(0)			(5)	30	17	3.0
Hemicycliophora conida	(0)			(0)			(4)	26	14	3.0
Total plant feeders		357 ᵃ	75		267 ᵃ	42		388 ᵃ	56	
Mean number of taxa		6.60 ᵃ	0.67		6.63 ᵃᵇ	1.02		9.20 ᵃ	0.74	
Mean maturity index		2.87 ᵃ	0.03		2.88 ᵃ	0.03		2.88 ᵃ	0.02	
Idem excl. Tylenchidae		2.97 ᵃ	0.02		3.02 ᵃᵇ	0.01		3.12 ᵇ	0.04	

late *Hippophaë* stage than in the early primary stage (Table 3). The maturity index for the total plant-feeding nematode fauna ranged from 2.57 at site 4 to 3.19 at site 21 (both late *Hippophaë* stage). Means for each successional stage (Table 3) were not different. However, when calculated only for obligate plant feeders (by excluding Tylenchidae), the maturity index increased significantly towards the later stages.

Nematode - environment ordination

Parameter sets for Canonical Correspondence Analysis (CCA) indicated by the letters A, C and E (Table 4) exclude factors that were correlated by $R > 0.67$ ($p < 0.001$), $R > 0.52$ ($p < 0.01$) and $R > 0.41$

($p < 0.05$), respectively. Substitution of factors by their excluded correlatives hardly affected the results of the analysis. Sets B, D and F were derived from the sets A, C and E by eliminating parameters which were not significantly ($p < 0.05$) correlated with one of the first four environmental axes of the CCA.

The selection of parameters led to improved significance of the canonical axes, and a higher trace per parameter (Table 5). Thus, parameters which were eliminated appeared to be less important. Redundance analysis (RA) resulted in non-significant ordinations, which implies that most taxa had a unimodal rather than a linear response to the environmental gradients. The results of CCA using nematode numbers were inferior to those of percentages.
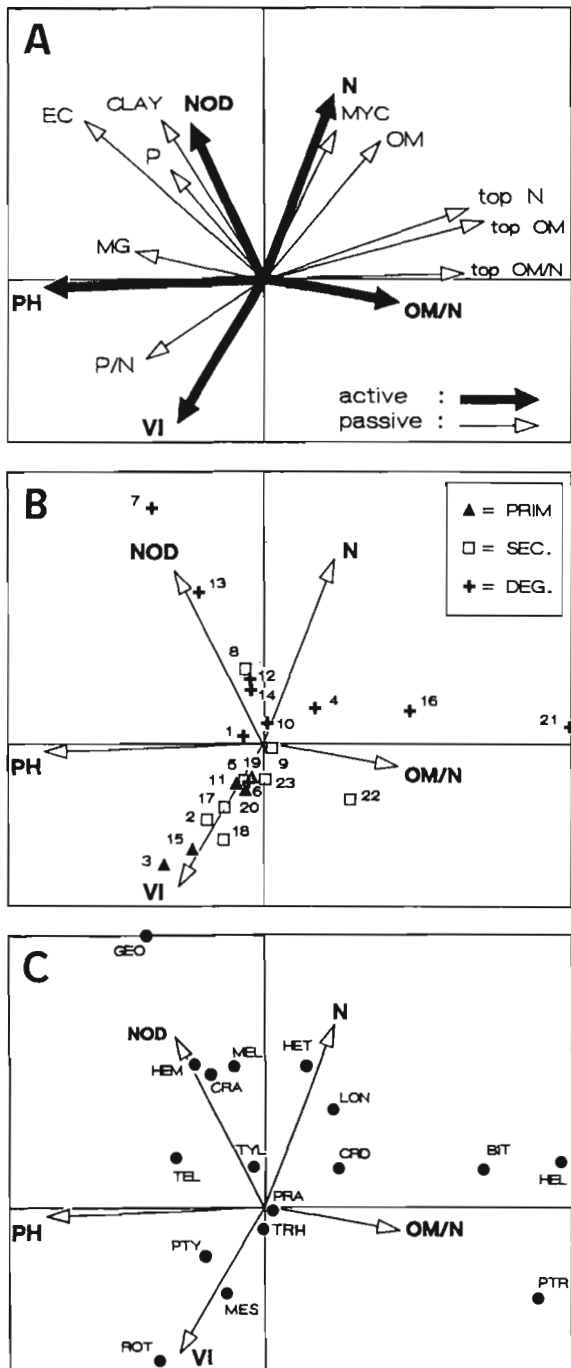
Table 4. Coefficients of correlation (R) of significant simple linear correlations between environmental parameters. See methods for explanation of parameter codes 1 to 21. N = 23; if R > .41 then p < 0.05, if R > .52 then p < 0.01, if R > .67 then p < 0.001. Non-significant coefficients are not shown.

Parameter nr. code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Parameter sets used in CCA
10-70 cm																						
SOIL LAYER																						
1 PH	1																					ABCDEF
2 P	.63	1																				AB
3 N			1																			ABCDEF
4 OM			.95	1																		
5 LIME	.68	.87			1																	
6 MG	.78	.73			.90	1																
7 K					.52	.50	1															A C E
8 NA	.50	.55	.58	.59	.55	.44	.42	1														A
9 EC	.92	.78			.80	.86		.68	1													
10 P/N	.57	.53	-.56	-.59	.52	.50			.46	1												AB
11 OM/N				.51							1											ABCDEF
12 PSM	-.49	-.55			-.65	-.76			-.55		.61	1										A C
13 CLAY	.52	.79			.74	.70			.70			-.75	1									
TOP SOIL																						
14 N			.68	.76						-.56	.45			1								
15 OM	-.42		.60	.70						-.53	.44			.99	1							AB
16 EC	.46	.65	.42	.43	.70	.67	.44	.66	.71				.48	.45		1						A C
17 P/N	.47	.49	-.42	-.49	.43					.81				-.63	-.59		1					C D
18 OM/N	-.60	-.44			-.43	-.47			-.49	-.43				.70	.78		-.56	1				
PLANT																						
19 VI																			1			ABCDEF
20 MYC																			-.44	1		ABCD
21 NOD								.42													1	ABCDEF

Table 5. Quality of ordination by Canonical Correspondence Analysis (CCA) or Redundance Analysis (RA) using percentages or numbers of plant feeding nematode taxa. Parameter sets A to F include environmental parameters as indicated in Table 4. The quality is expressed as the level of the eigen value of the first canonical axis and of the sum of eigen values (trace) of all axes, and the probability of achieving these levels in a Monte Carlo Random Permutation test. * = p ≤ 0.05; ** = p ≤ 0.01.

Method	CCA	CCA	CCA	CCA	CCA	CCA	RA	RA	CCA	CCA
% / nrs.	%	%	%	%	%	%	%	%	nrs.	nrs.
param. set	A	B	C	D	E	F	B	D	D	F
n variabl.	13	9	8	7	6	5	9	7	7	5
Eigen value first axis	0.50 *	0.50 *	0.50 *	0.49 **	0.40 *	0.38 *	0.19 ns	0.17 ns	0.48 **	0.36 *
Trace	2.08 ns	1.70 *	1.70 ns	1.36 *	1.00 *	0.94 *	0.69 ns	0.44 ns	1.30 ns	0.92 ns

The ordination of sites (Fig. 1 B) shows that sites of the early primary succession type are all situated in the lower left quadrant. Sites with early secondary succession are below the first axis, except for site 8 (sludge deposit). The sites below the first axis are predominantly mono-vegetations of *Hippophaë*. Old stable sites with degenerating scrubs are above the first axis, except for site 6, which has developed from sand with a low lime content ($< 2 \% CaCO_3$). Above the axis only mixed vegetations with *Hippophaë* are found; in the top right quadrant are two damp slacks and a typical dune meadow site, whereas in the top left quadrant the mixed scrubs and sites with a poor vegetation are located. The environmental optima of the nematode taxa (Fig. 1 C) are arranged roughly along the same lines as the sites.

Linear nematode - environment correlations

R. goodeyi was found in higher numbers under vigorous *Hippophaë* scrubs (Table 6), whereas numbers of *L. dunensis* tended to be higher under degenerating scrubs (p = 0.10). *Meloidogyne* spp. and *L. dunensis* were correlated positively with total P and lime. Higher numbers of these two taxa and of *H. pseudorobustus* and *Pratylenchus* were found when total N or organic matter was higher. Most of the correlations which were found using nematode numbers (Table 6) were also found when relative abundances of taxa (percentage of total plant-feeding nematodes) were used. This indicates that effects on the total number of plant feeders did hardly affect the proportion of the major taxa.

Nematode - nematode correlations

Significant (p < 0.05) negative correlations were observed between abundances of *R. goodeyi* and *T. microphasmis* and between *M. xenoplax* and *Pratylenchus* spp. Positive correlations were found between *H. pseudorobustus* and *Pratylenchus* spp. (p < 0.05), between *Meloidogyne* spp. and *Pratylenchus* spp. (p < 0.05), and between *L. dunensis* and *Pratylenchus* spp. (p < 0.01). *H. pseudorobustus*, *Paratrichodorus* spp. and total plant feeders were correlated due to their high number in an old slack (site 21).

Passive ordination of excluded environmental parameters (Fig. 1 A) shows the imaginary position of these parameters in the simplified force field. Nearly identical or opposite direction of vectors does not always imply correlation between two factors. It may also reflect a similar or inverse relation, respectively, with the nematofauna.

Fig. 1. Results of Canonical Correspondence Analysis of nematofauna and five selected environmental factors. Ordination of environmental parameters, sites and nematode optima on the first two canonical axes. A : Environmental parameters; for parameter codes see methods; B : Sampling sites (symbols indicate successional stages : PRIM = early primary, SEC = early secondary, and DEG = degeneration stage; site numbers refer to those in Table 1.); C : Canonical optima of nematode taxa (codes are the first three letters of the genus name, except for : Cra = *Criconema*, Crd = *Criconemoides*, Pty = *Paratylenchus*, Ptr = *Paratrichodorus*, and Trh = *Tylenchorhynchus*).

Table 6. Nematode numbers - environmental factors correlations. Coefficients of significant correlations are given; n = 23, if R > .41 then p < 0.05, if R > .52 then p < 0.01. Nematode data were either original or log (x + 1) transformed (largest R is shown). Taxa and factors that are not shown had no significant correlations.

Taxon	PH	P	N	OM	LIME	K	NA	P/N	VI
Rotylenchus goodeyi	.	.	.	.	.	.49[1]	.	.	.48
Mesocriconema xenoplax	.	.	.	.	.	.48[1]	.	.	.
Meloidogyne spp.	.42	.55	.64	.54	.52	.	.46	.	.
Pratylenchus spp.	.	.	.51	.45	.	.	.	.	.
Paratrichodorus spp.	− .49[1]	.	.	.	.	.	.	.	.
Helicotylenchus pseudorobustus	− .56	.	.48	.53	.	.	.	− .48	.
Longidorus dunensis	.	.48	.43	.	.43	.	.	.	.
Total plant feeders	.	.	.42	.	.	.	.	.	.

([1]) Correlation due to one deviating sample.

Table 7. Nematode densities (per 100 g soil) on a succession transect at Schouwen. Sites (see also Table 2.) : A. *Elymus arenarius;* B. *Ammophila arenaria;* C. *H. rhamnoides* (invading); D. *H. rhamnoides* (degenerating); E. *Ligustrum vulgaris.*

Nematode taxon / Site	A	B	C	D	E
Rotylenchus goodeyi	0	1	0	5	0
Paratylenchus spp.	1	1	0	0	+
Mesocriconema xenoplax	0	3	10	3	6
Tylenchorh. microphasmis	0	+	2	29	1
Heteroderinae (juv. 2)	5	0	0	3	+
Tylenchidae	8	13	82	4	9
Telotylenchus ventralis	2	+	0	1	0
Pratylenchus spp.	1	1	3	4	9
Bitylenchus dubius	0	0	0	8	0
Paratrichodorus spp.	0	0	0	1	32
Helico. pseudorobustus	0	1	0	238	17
Longidorus dunensis	0	0	0	21	3
Hemicycliophora conida	+	0	+	0	0
Total plant feeders	15	19	97	317	78
Maturity index	2.48	2.28	2.15	3.12	3.37
Idem excl. Tylenchidae	2.94	2.86	3.00	3.14	3.54

(+ = present, but less than 1 per 100 g soil).

TRANSECT SAMPLING

Highest numbers of most taxa were found under the degenerating *Hippophaë* scrub at a meadow border (Table 7). *M. xenoplax* had a maximum in an earlier stage and *Paratrichodorus* spp. and *Pratylenchus* spp. in a later stage. *L. dunensis, Paratrichodorus* spp. and *B. dubius* were not found on the pre-*Hippophaë* sites.

RHIZOSPHERE SAMPLING

T. microphasmis was the dominant species in the area, which is in agreement with the field survey results. Den-

sities of *R. goodeyi* and *M. xenoplax* in the bulk soil on the seaward dune ridge were lower than at comparable sites in the field survey. For most taxa, the density in the rhizosphere was much higher than in the bulk soil (Table 8). Generally, the ratio rhizosphere/bulk soil was higher in the inner dune sites compared to the sites on the seaward ridge. In a few cases (*e.g.* for *H. conida*) a lower density was found in the rhizosphere than in the bulk soil.

Table 8. Plant feeding nematodes in *Hippophaë* seedling rhizosphere (R) and bulk (B) soil. Numbers per 100 g soil. Locations : 1. seaward ridge, between degenerating *Ammophila;* 2. id., between vigorous *Hippophaë;* 3. inner dunes, between degenerating *Hippophaë;* 4. id., grasses post-*Hippophaë* stage.

Taxon	Location			
	1 R/B	2 R/B	3 R/B	4 R/B
Rotylenchus goodeyi	4/ 1	6/ 2	0/ 1	17/ 1
Mesocriconema xenoplax	0/ 1	3/ 4	0/ 2	17/ 2
Tylenchorh. microphasmis	196/37	245/72	498/28	503/34
Tylenchidae	5/ 1	44/ 3	36/ 1	1418/27
Pratylenchus spp.	22/ 1	15/ 1	102/ 1	0/ 0
Longidorus dunensis	0/ 0	0/ 0	32/17	4/ 4
Paratrichodorus spp.	3/ 0	0/ 1	12/ 2	0/ 2
Hemicycliophora conida	0/11	0/ 0	0/ 0	0/ 0
Ratio rhizosphere/bulk soil	4.4	3.8	13.1	28.0 **
Final shoot biomass (g)	4.65	3.98 ns	3.86 *[1]	3.47 **

([1]) Significantly different from location 1. : * = p < 0.005; ** = p < 0.01.

Densities in rhizosphere soil were higher at the inner dune sites, especially in the case of *T. microphasmis*, Tylenchidae and *Pratylenchus* spp. Population densities in bulk soil were not much different between sites, except for the higher level of *T. microphasmis* in the vigorous *Hippophaë* scrub and the absence of certain taxa at some locations. *Pratylenchus* spp. were very much concentrated in the rhizosphere, and thus their numbers may have been largely underestimated in the field survey and transect samplings.

Discussion

ENVIRONMENTAL DEVELOPMENT

Development of environmental characteristics in *Hippophaë* vegetations proceeds along the vigour- and nitrogen vectors, rather than exactly along one of the nematode-environment axes (Fig. 1). From the primary succession stage with low soil-N concentrations and high *Hippophaë* vigour, locations develop (directly, or after disturbance and secondary succession) towards a stable state with higher concentrations of total N. There is a divergence of sites in the degeneration stage, either towards a lower pH and an increased ratio organic matter/N (dune slacks and meadows), or towards an increased *Frankia*-nodulation potential (NOD) (mixed scrubs on calcareous sites). The ecological meaning of NOD is not clear, but it probably reflects the duration and intensity of the *Frankia-Hippophaë* symbiotic history of a certain site (Oremus, 1979).

Of the five most important environmental factors in the ordination, pH and total N are correlated with a number of other factors (Table 4), and thus positions of sites or nematode taxa might (albeit less strongly) also be attributed to those other factors.

NEMATOFAUNA DEVELOPMENT

Dune ageing and vegetational development are accompanied by development of the plant-feeding nematode fauna. The number of taxa and the maturity index of this trophic group increase (Table 3), because species with slower dispersal, longer generation period, and larger body size *(e.g. L. dunensis)* or less resistance to environmental stress *(e.g. Paratrichodorus)* become more abundant (Bongers, 1990). This may proceed partly at the expense of species with opposite characteristics *(e.g. Paratylenchus* spp., *R. goodeyi* and *M. xenoplax)*. The significant difference between maturity indices of obligate plant-feeding nematofaunas of different *Hippophaë* stages shows the sensitivity of the maturity index as a measure of ecosystem stability and long-term development.

Paths of nematofaunal succession can be derived from taxon optima in the ordination (Fig. 1 C). The " average " development proceeds from *R. goodeyi* in the young primary stage soils, through successive optima of *M. xenoplax*, *Paratylenchus* spp., *T. microphasmis* and *Pratylenchus* spp. to *L. dunensis* and others under

degenerating scrubs on old stable dunes. As in the edaphic development, there is also some divergence in the nematode fauna. This is mainly due to a few sites which deviate both in environment and in nematofauna. The ordination of *Paratrichodorus* spp. was largely affected by the high abundance of *P. pachydermus* in an old dune slack (site 21). *B. dubius* was found mainly at a decalcified dune meadow site (16). Conversely, *G. arcticus* was found almost exclusively under degenerating *Hippophaë* vegetations on dry calcareous soil (sites 7 and 13).

Ordination of environment, sites and nematofauna by canonical correspondence analysis (CCA) appeared a useful way to visualize successional changes and ecological associations. The better results of CCA compared to redundance analysis indicate that nematodes have unimodal rather than linear responses to the selected environmental factors. Relative abundances of taxa (percentages) were more informative in CCA than numbers (Table 5), probably because the number of plant-feeding nematodes had more residual variation than the species composition of the nematofauna. Comparison of numbers and percentages in linear nematode - environment correlation supports the conclusion from CCA that variation in the total number of plant-feeding nematodes hardly affects the species composition.

NEMATODE DISPERSAL AND NICHE DIFFERENTIATION

For plant-feeding nematodes, the presence and productivity of their host plants are the chief determinants of population densities (Yeates, 1987). However, in the relatively young dune soils the presence of nematode species for which *Hippophaë* is a good host seems largely determined by accidental arrival and subsequent colonization. Growth of *Hippophaë* is optimal in the early stages, and thus high densities of *Hippophaë*-feeding nematode species would be expected if they were present all over the site and if environmental constraints were not stronger than in later stages.

In the present survey some taxa were not found in the early primary stage (Table 3). One could conclude that *R. goodeyi*, *M. xenoplax* and *T. microphasmis* are much better dispersed than *L. dunensis*. One of the reasons for this may be that *L. dunensis*, contrary to *e.g. T. microphasmis*, is almost absent from the top 10 cm of soil (F. C. Zoon. unpubl.). Taxa which are present in the top soil and which are more resistant to dehydration are more easily dispersed by wind (Gaur, 1988) or biotic vectors. Active dispersal through the soil generally takes place at a rate of less than a meter per annum. Dispersal by man, the major means of nematode colonization in new polders (Kuiper, 1977), may be important for nematode species present in the rhizosphere of Marram grass [*Ammophila arenaria* (L.) Link], which is used as planting material in coastal defence practice.

The ability of species to colonize preceding vegetations may also contribute to their presence in early *Hip-*

pophaë stages. Populations of *R. goodeyi*, *Pratylenchus* spp., *Paratrichodorus nanus* and Tylenchorhynchinae (*Telotylenchus ventralis* and *T. microphasmis*) were found on outer dune locations with a vegetation of *Ammophila arenaria* (van der Putten, 1989). These taxa, as well as *M. xenoplax*, *Helicotylenchus pseudorobustus* and *Hemicycliophora conida* were also found at some pre-*Hippophaë* sites in the present study. Species found at these sites presumably feed on *Ammophila*. *Pratylenchus* sp. was able to multiply on *Ammophila* in a pot experiment (van der Putten, 1989).

Coefficients of variation of the mean population density of taxa generally increased during succession, only in the case of *M. xenoplax* and *T. microphasmis* it decreased. The rise in variation may be due to an increasing difference between environmental constraints of sites, or to an increasing clustering of nematode subpopulations within sites together with the development of mixed vegetations. The latter may result in site compartments with near maximal densities of preferentially *Hippophaë*-feeding nematodes, alternating with compartments having much lower densities. The decrease in variation observed for *M. xenoplax* and *T. microphasmis* may be attributed to incomplete colonization of many early stage sites, and little response to changing soil and vegetation characteristics in later stages. Both of these species remain present in fairly high densities in later *Hippophaë* stages.

The possible role of changing environmental constraints can only partly be explained by the results of the present study. Plant-feeding nematode taxa exhibit a certain optimum during the course of succession as is illustrated by the SOP in Table 3 and in the results of CCA. The optimum for a taxon as found by CCA (Fig. C) corresponds to environmental factors, which are not necessarily functionally related to the presence or abundance of a taxon. The correlation of *Meloidogyne* and *H. pseudorobustus* with total N and organic matter (Table 6) may be due to the fact that better host plants (grasses) are present in the late *Hippophaë* stages. The development of the herbaceous undergrowth can determine the nematode fauna to a great extent as was found in tree nurseries (Niblack & Bernard, 1985). However, the positive correlation of different taxa and of the total number of plant feeders with total N (Table 6) may also have a functional background in the food quality (Yeates, 1987). The association between *Longidorus dunensis* and nitrogen may be related to its slow dispersal and late arrival under *Hippophaë*. On the isle of Texel, *L. dunensis* was not found, in spite of high ultimate levels of total N.

It seems that the edaphic factors studied do not directly explain the presence or absence of the major taxa. Nevertheless, they do correspond to the relative abundance of taxa within the plant-feeding nematode community and they may be key factors in the regulation of population densities. Especially, the nitrogen availability, which in the early stages limits plant growth (Willis & Yemm, 1961; Vitousek & Walker, 1987) will be even more limiting to nematodes, as these have a lower C/N ratio than plants (White, 1984; Yeates, 1987). This may also explain the lower density of *T. microphasmis* in the rhizosphere of seedlings planted at the foredune sites (Table 8). The content of available nitrogen in soil at these sites was about 10 meq/kg, compared to 20 meq/kg at the inner-dune sites (Zoon, unpubl.).

The negative correlations *R. goodeyi-T. microphasmis*, and *M. xenoplax-Pratylenchus* spp. in the survey may indicate interspecific competition or differential host preference. From what is known about the feeding habits of these or congeneric taxa, and their feeding sites on the root (Klinkenberg, 1963; Wyss, 1981) competition seems possible. For reasons discussed above, the statement that plant-feeding nematodes are usually not resource limited, and therefore seldom compete for common resources (Norton, 1989) appears to face exceptions in sand dune ecosystems.

HIPPOPHAË RHAMNOIDES AS A HOST PLANT

Many of the plant-feeding nematode species found under *H. rhamnoides* are able to multiply on this shrub species. Populations of *T. microphasmis* increased by a factor 5 within four weeks after inoculation in sterilized sand in greenhouse pot experiments with *Hippophaë* seedlings (Maas *et al.*, 1983). For *L. dunensis* the same authors found multiplication by a factor 3.5 in four weeks, but a factor 9 was found if lower densities were inoculated in large soil columns (Zoon, unpubl.).

M. xenoplax is a parasite of various woody and herbaceous plants especially in sandy soils (Knobloch & Bird, 1978; Nyczepir & Lewis, 1984; Zehr *et al.*, 1986; Güntzel *et al.*, 1987). Pot experiments with different nematode species (Zoon, unpubl. res.) show that *M. xenoplax* is also able to multiply on *Hippophaë* (from 20 to 27 000 per dm^3 soil in 6 months). A population of *P. pachydermus* increased from 20 to 6000 within 6 months, but *H. pseudorobustus* failed to multiply substantially (from 20 to 70 in 6 months). In the present study, no root knots or cysts were observed on *Hippophaë* roots isolated from the field, indicating that the Heteroderidae species present do not feed on *H. rhamnoides*.

The ratio rhizosphere/bulk soil (Table 8) can also give an indication of the host preference of a nematode species. In addition to the host relations mentioned above, *Pratylenchus* spp. appear to prefer *Hippophaë*, whereas *Hemicycliophora conida* seems to avoid this plant. The latter confirms observations by Kuiper (1977) that woody plants, such as apple and pear trees are non-hosts for *H. conida*.

Population densities of nematodes on a soil volume basis (Tables 3 and 7) were low in these dune soils when compared to agricultural soils. This is probably due to

the very diffuse rooting in the poor dune sands and the low level of primary production. However, nematodes may be considered harmful on a root length basis. The sampling of bulk soil greatly underestimated the number of *Pratylenchus* spp. in the rhizosphere. Densities of *T. microphasmis* and *M. xenoplax* in bulk soil were relatively high on a site closely surrounded by vigorous *H. rhamnoides* (site 2 in Table 8), probably because there were many *Hippophaë* roots present. No other plant species were present at this site.

Growth reduction of the *Hippophaë* seedlings (Table 8) seems to be related to the population density of *T. microphasmis* in the rhizosphere (p = .14). The pathogenicity of this nematode towards *H. rhamnoides* is evident from pot experiments (Zoon, unpubl.). As discussed above, higher availability of soil N may be favourable for nematode populations, but in addition, root damage by nematodes and the subsequently reduced uptake of P by the host plant (Zoon, unpubl.) might also increase the N concentrations in the root tissues, thus offering a better food quality for nematodes. It seems possible that nematodes and other root herbivores do not only increase the food quality for foliar-feeding herbivores (Gange & Brown, 1989), but also for themselves. Nonetheless, the root damage may lead to degeneration or loss of competitive ability. The ordination (Fig. 1) shows that low vigour of *Hippophaë* is associated with high N, OM and MYC and with low P:N ratio. The increased mycorrhiza (MYC) is an indication for P-limitation (Menge *et al.*, 1978). Therefore, we suggest that the change in the balance of nutrient resources (N and P) may be the ultimate factor in this succession (Tilman, 1982), whereas plant-feeding nematodes may be the proximate factor by interfering with the plants nutrient uptake capacity.

Nematode - host relationships with other plant species of late- and post- *Hippophaë* stages were not studied extensively. It appears that *H. pseudorobustus* is associated with graminaeous hosts which often form the undergrowth of degenerating *Hippophaë* scrubs. Multiplication on *Hippophaë* in pots was negligible. Numbers of *L. dunensis* were lower at sites of the post-*Hippophaë* stage than in the preceding degeneration stage (Tables 7, 8), but it is not clear wether this is due to the appearance of inferior hosts.

In conclusion, this study has demonstrated that during natural development of soil and vegetation there can be a considerable development of the plant-feeding nematode fauna, even if the dominant plant species remains the same. This process may be of importance for the decline of *H. rhamnoides* and for the rate and direction of vegetational succession in general.

Acknowledgments

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