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Effects of sand movement by wind on nematodes and soil-borne fungi in coastal foredunes

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Abstract. In stabilized dunes *Ammophila arenaria* (marram grass) degenerates due to a process involving soil-borne pathogens and parasites. This leads to exposure of the sand surface so that wind erosion may create blowouts. *Ammophila* rejuvenates on the edges of the blowouts, where the sand has accumulated. We tested the hypothesis that such rejuvenation of plants may be related to a reduction of the plant-parasitic nematodes and fungal propagules during the process of wind-driven transport.

Field measurements in blowouts during storm events indicated that the drifted sand contained relatively low numbers of plant pathogenic fungi and plant-parasitic nematodes. A wind tunnel experiment showed that drifting sand may indeed reduce the numbers of fungi and nematodes. Although most fungi were attached to sand particles, they were also affected by the wind-borne sand movement. Sand that had been deposited by wind was made up of a larger proportion of large-sized particles. In our experiment the relatively small particles were lost during transport.

Stirring the soil (part of the forces of natural winds) by mixing for 15 min. with a propeller mixer at 1500 rpm significantly reduced the number of nematodes and fungi. Both sand movement in the wind tunnel and intensive stirring of the sand enhanced the growth of *Ammophila* test plants in a bioassay. It was concluded that in wind-blown sand the pathogen inoculum is reduced. Therefore, serious consideration should be given to allowing controlled reactivation of blowouts to rejuvenate declining *Ammophila* in stabilized foredunes.

Implications for dune management are briefly discussed.

Keywords: Aeolian transport; *Ammophila arenaria*; Blowout; Sand supply; Rejuvenation; Soil-borne disease.

Nomenclature: van der Meijden (1990) for vascular plants. Nematodes were identified to the genus level according to Bongers (1988). The allocation of nematodes to feeding groups was according to Yeates et al. (1993). Nomenclature of fungi according to Domsch et al. (1980) was used throughout this study except for *Fusarium*. Species of the latter genus were identified according to Nelson et al. (1983).

Introduction

Wind-driven sand movement is one of the most conspicuous abiotic characteristics of coastal foredunes. Vegetation plays an important role in trapping the sand (e.g. Olson 1958; Ranwell 1972; Willis 1989). In European coastal foredunes Marram grass (*Ammophila arenaria* (L.) Link) is the dominant sand-trapping plant species (Huiskes 1979). In North-America and Canada the American Beachgrass, *A. breviligulata* Fern., is one of the most important sand-fixing species (Eldred & Maun 1982; Maun 1984; Maun & Lapierre 1984; Baye 1990). The vigour of both plant species is highest on beach-facing slopes where fresh wind-blown beach sand regularly accumulates. Both species degenerate when sand accumulation diminishes (Marshall 1965; Hope-Simpson & Jefferies 1966; Huiskes 1979; Disraeli 1984; Maun & Lapierre 1984; Willis 1989; Baye 1990). Several factors have been reported to be involved in the decline of *Ammophila* at stabilized sites. Among them are infections by plant-pathogenic soil organisms, particularly nematodes and fungi (van der Putten et al. 1990; van der Putten & Troelstra 1990; de Rooij-van der Goes 1995).

Severely degenerated stands are vulnerable to erosion. This may endanger the stability of the dunes that serve as natural seawalls. Rejuvenation of declining *Ammophila* is known to occur when the degenerated vegetation is exposed again to deposition of fresh wind-blown sand originating from the beach (Hope-Simpson &Jefferies 1966; Willis 1989). In the inner dunes, however, rejuvenation also occurs along the edges of blowouts, i.e. erosion hollows within the dune complex (Carter et al. 1990) where sand accumulates (van Dieren 1934; Willis 1989).

Blowouts usually start at sites where the vegetation is almost absent (Jungerius & van der Meulen 1989, 1997; van Boxel et al. 1997). The soil surface of sand dunes may still be fixed by algae, mosses or microbial mats (Pluis & de Winder 1990) but after

disturbance of the soil surface (for instance by animal activity or rainfall) superficial sand deflation can occur which may start the erosion process. Further deflation increases the size of a blowout (i.e. saucer blowouts), usually in the opposite direction to prevailing winds (Jungerius & van der Meulen 1989; Carter et al. 1990). Upwind expansion is not common in through-blowouts (see Hesp 1996). Aeolian transport may start when the wind-velocity exceeds a threshold value, which is about 6 m/s in the case of dry sand (Bagnold 1954).

Previous studies showed that burial with sand containing plant-pathogens and parasites is less beneficial for the plants than burial with sand free of these soil organisms (de Rooij-van der Goes et al. 1995a). In the present study, we hypothesized that restored vigour along the edges of blowouts correlates with a reduction of soil-borne pathogens and parasites during sand drift. The same was also suggested in the case of the regeneration of Sea buckthorn (*Hippophaë rhamnoides* L.) after soil disturbance (Zoon et al. 1993).

Sand can be transported by wind in three ways: in suspension in dusts (usually smaller than sand-sized particles), by bouncing/saltation or by rolling. Therefore, during long distance transport of the material in which the sand is suspended, the nematodes and fungi may either be physically separated from the sand or they may die when scoured between sand grains. Thus, sand that is deposited on the vegetation is assumed to be less infested by pathogens and parasites than the original sand from the deflation site.

In this study, the hypothesis that numbers of pathogenic soil organisms in dune sand previously covered by *Ammophila* may be reduced as a result of sand movement by wind has been tested. A pilot study on nematodes and fungi in wind-driven sand originating from blowouts indicated low concentrations of these organisms. It was impossible to trace the original sand so that no estimation could be made of the actual elimination of soil organisms. Therefore, it was decided to perform an experiment in a wind tunnel. Furthermore, the effects of a component of aeolian transport (scouring of sand particles) on numbers of pathogenic soil organisms was simulated and tested under laboratory conditions.

The results of such a study have a clear bearing on the management of coastal sand dunes, in particular as far as the balance between fixation and reactivation is concerned.

Methods

Drifting sand in blowouts

On January 18th 1994, drifting sand was trapped in a blowout (45m $\times$ 27 m width) in the calcareous foredunes of Goeree (The Netherlands) at km-landmark 18.75 (51°48' N, 3 °52'E). That day, the wind direction was dominantly southwest with a velocity of 7.5-13m/s (weather report of the Royal Netherlands Meteorological Institute).

The sand traps used consisted of cotton bags (mesh size ca. 100 µm), with an opening of 5 cm $\times$ 25 cm and 25 cm deep (after Draga 1983). The bags were placed at 5, 15, 25, 35 and 45 cm above the sand surface in a metal frame which was anchored in the soil. To collect drifting sand all traps were directed with openings facing the prevailing wind. The traps were placed in a fixed pattern: at the centre of the blowout, halfway up the deposition slope and on top of the deposition lobe (Fig. 1). Sand was trapped during a period of 6 h whereafter the contents of each bag was weighed. One additional (control) soil sample, consisting of three subsamples of approximately 150 ml, was taken by using a scoop from the top 10 cm layer at the deflation site of the blowout. All trapped sand was analysed as one large sample. The trapped sand and soil from the deflation site was analysed to determine the species of fungi and nematodes as well as their abundance.

The fungi were isolated according to Warcup (1960) on malt extract agar, containing 20 g malt extract (Oxoid), 3 g pepton (Oxoid), 15 g agar (Merck) and 2.5 g bile (Sigma) with 100 ppm oxytetracycline per litre of tap water. In contrast to the additional samples taken from the deflation site, the amount of sand in the cotton bags was too small to allow analysis of nematodes by elutriation (Oostenbrink 1960). Therefore, 10 g of soil from each bag was spread over an extraction dish and placed in 100 ml of tap-water for 48 hours (Hooper 1986) after which the nematodes were identified and counted. The other samples were examined in triplicate by elutriation (Oostenbrink 1960), identified and counted.

Soil samples

In February and August 1993 soil was collected from the root zone of vigorous *Ammophila arenaria* stands in the foredunes of Voorne, The Netherlands, at a site immediately north of the Haringvliet dam (51°52'N, 4 °04'E) for the following experiments. The samples were taken from 15 random sites in an area of 600 m^2 and originated from the layer between 5 and 40 cm below the surface containing one and two-year old roots of *Ammophila*. The sand was gently

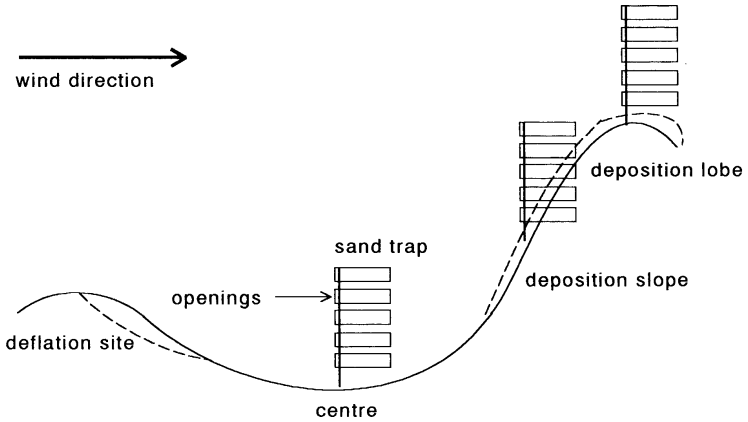

Fig. 1. Schematic view of a blowout with sand traps. The development of the blowout is presented by the dotted line.

sieved (mesh size: 2cm) and homogenized. Sifted roots were chopped into 2-5cm pieces and mixed with the soil. Part of the collected soil was sterilized by gamma-radiation (4 Mrad).

Sand movement by wind in a wind tunnel

The effects of wind-driven sand movement on numbers of nematodes and fungal propagules was experimentally tested in a wind tunnel. The tunnel was 75 cm wide, 75 cm high and 15 m long. The wind speed could be set between 0 and 28 m/s (0 to 10 on the Beaufort scale). In the wind tunnel, soil was blown at a velocity of 22 m/s (scale 9 Beaufort). A total of 50 kg of soil was collected in August 1993, half of which was blown in the wind tunnel. The initial moisture content of the blown sand was 4% (weight/weight) (field humidity). It was not dried prior to the experimental treatment. Soil was spread on a 1 m × 0.75 m plate in a 2 cm thick layer. The plate was positioned on the floor at the entrance of the wind tunnel. The wind speed was slowly aumented to the desired level. The wind-blown soil was caught in traps of six cotton bags each (similar to those used in the field experiment). The outer frames of the traps were 60 cm wide and 40 cm high thus covering about half the wind tunnel cross section. Three traps were placed at 4, 8 and 12 m distance from the source. After all the soil had been blown from the plate, the wind speed was slowly reduced to zero. The wind-blown soil was collected from the bags in the traps and from the wind tunnel floor near the trap. The soil was collected in one large sample and analysed.

Particle size distribution: air-dried wind-blown and non-blown soil, discarded from roots, was sieved through mesh sizes of 600, 425, 300, 212, 150 and 75 mm, respectively. This was done in duplicate.

Soil-organisms: in order to establish potential relationships between particle size and species of fungi, small amounts (0.03 ± 0.002 g) of soil collected from each mesh size were plated in triplicate on malt-extract-agar to isolate the fungi (Warcup 1960). Fungi were also isolated in triplicates according to Warcup (1960) on malt-extract-agar from the total sample of wind-blown and non-blown sand. The numbers of the various species of nematodes in 100 ml of wind-blown and non-blown sand were assessed after collecting them in duplicate by elutriation (Oostenbrink 1960).

Pot-experiment: the effect of soil sterilization of wind-blown and non-blown soil on the productivity of *Ammophila* was studied in a pot-experiment in order to assess and compare the degree of pathogenicity between treated and untreated soil. Seeds collected from a vigorous stand at Voorne were germinated on glass beads at an 8/16 hour dark/light regime at 10/30 °C. Pots of 1.5 l were filled with 1500 g soil (10% soil moisture (w/w)) and each treatment was repeated six times. Each pot was planted with six two-week-old seedlings (3 to 5 cm tall). The sand surface was covered by aluminium foil to prevent desiccation of the sand. The pots were placed in a greenhouse at 23 °C (± 2 °C). A day length of minimally 14 h was achieved by additional illumination (250 µmol m^{D2} h^{D1}). Once a week, the soil moisture content was set at 10% (weight/weight) with demineralized water. To avoid nutrient deficiency during plant growth, increasing amounts of nutrients were added: weeks 1 to 4: 15 ml and weeks 5 and 6: 25 ml full strength Hoagland nutrient solution. After two weeks, the plants were randomly thinned to a density of four plants per pot. The plants were harvested after a growing period of six weeks. After harvesting, shoot- and root-weights were determined after drying at 70 °C for 48 h. Nematodes in soil were counted and identified after decanting the whole pot (Oostenbrink 1960).

Effects of scouring

In February 1993, 75 kg of soil from the root zone of *Ammophila arenaria* was collected. To study the effects of scouring on the numbers of nematodes and fungi, the soil was stirred using a propeller mixer for 15 minutes at a velocity of 0, 300, 600, 900 or 1500 rpm, respectively. During stirring, soil temperatures increased from 10-15 °C to about 20 °C.

A pot experiment with the same soil (after mixing) was performed with a similar design to that in the wind-tunnel experiment. Five replicate pots were filled with the non-mixed soil. The pots were planted with seedlings of *Ammophila* and harvested after eight weeks. A control with non-mixed sterilized soil was also included. The growth of *Ammophila* seedlings was compared with that in non-mixed, unsterilized and sterilized soil. If soil samples were analysed directly after scouring, damaged nematodes might also be recovered; therefore, a time lag of four days was used after which the numbers of nematodes were assessed. This was done by decanting (Oostenbrink 1960) using three replicate pots per mixing treatment.

Fungi were isolated by soil-dilution before the pot-experiment started. For soil dilutions, 10 g of dry soil was suspended in 90 ml of sterilized water. One ml of the dilutions 10^{D2}, 10^{D3} and 10^{D4} was spread in triplicate on malt-extract-agar. At harvest, nematodes were isolated by decanting the whole pot (Oostenbrink 1960).

Data analysis

The biomass data and nematode numbers of both pot experiments and the number of fungi of the stirring-experiment were analysed statistically by one-way analysis of variance after testing for normality of variances with CochranÕs*Q*-test. If required, the biomass data and the numbers of fungi were ln-transformed and numbers of nematodes were square-root-transformed in order to approach a normal distribution of the data. The treatment means were compared using TukeyÕs test ($P < 0.05$).

For the wind tunnel experiment, WilcoxonÕs rank sum test was used to analyse the effects of aeolian transport (wind-blown vs non-blown soil) on the dominant species of fungi. The Pearson rank correlation coefficient and correlation significances were calculated for correlations between the number of colony forming units of the most dominant fungal species and particle size. Significant differences were set at the 5% level.

Results

Drifting sand in blowouts

The blowout of Goeree was regularly visited during 1993 and the beginning of 1994 to collect wind-blown sand. Unfortunately, on only few occasions was sand being blown. Wind-driven transport took place only when a dry period was succeeded by moderately strong winds (6 Beaufort) and not, as was assumed, during heavy storms (9 Beaufort). On January 18th 1994 in the blowout at Goeree, sand was only trapped during one hour of the six hours measurement period, after which no further movement occurred. At the centre of the blowout and on the depositional slope, sand drifted just above the soil surface, whereas at the top of the depositional lobe, the amount of trapped sand was more evenly distributed over the different heights (data not shown).

The number of fungal propagules (counted as colony forming units) in soil trapped in the bags were insignificantly affected by the wind-driven sand movement compared to the numbers in soil collected from the deflation site of the blowout. The numbers were lower than those found in a vigorous stand (Table 1). Direct microscopic observations of the wind-transported sand caught on Petri-dishes containing 2% water-agar that were held against the wind for a few minutes showed that the majority of fungi and bacteria were attached to the soil particles (data not shown).

The living nematodes caught in the cotton bags were mainly non-plant-feeding nematodes. The dorylaimids (i.e. nematodes with a tooth in stead of a spear, consuming different kinds of food) and the very few plant-parasitic nematodes (with a spear) that were found in the trapped soil were dead. Nematodes seemed to be strongly affected by wind-driven sand transport (Table 1). This is similar to the situation in soil sampled from the surface (Table 1).

Table 1. Nematodes (numbers per 10 g dry soil) and fungi (number of colony-forming units, CFU, per g dry soil) in sand collected in the sand traps (combined over all traps), from the deflation site of the blowout and in the root zone of vigorously growing *Ammophila arenaria* at the sea-facing slope of the Goeree dunes. The blowout was sampled in January 1994. Data for the vigorous stand from de Rooij-van der Goes et al. 1995a (fungi) and de Rooij-van der Goes et al. 1995b (nematodes).

	Sand traps	Deflation site of blowout	Vigorous stand of *A. arenaria*
Fungi (CFUs)	1260	1460	1800
Nematodes	3	15	43

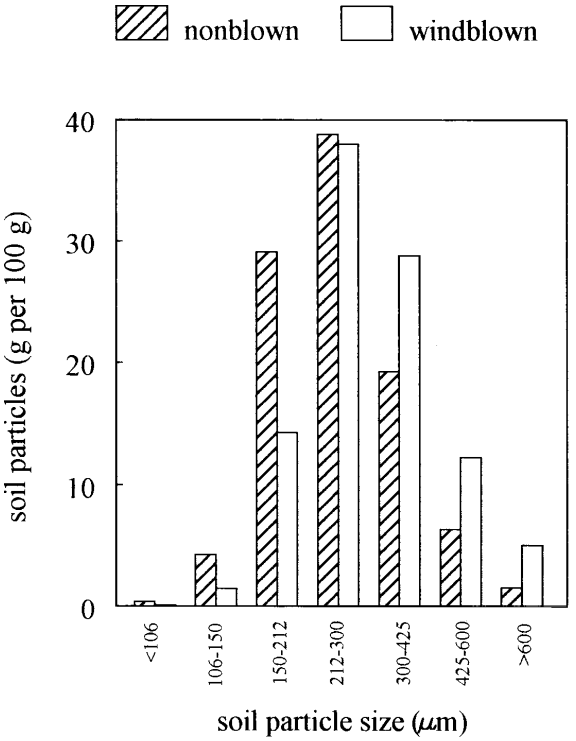

Fig. 2. Proportional particle size distribution of non-blown and wind-blown sand that was blown in a wind tunnel at a wind speed of 22 m/s. The data are means of two samples.

Sand movement by wind in a wind tunnel

The soil moisture content had decreased to a level of about 1 % in wind-blown soil when blown. Relatively moist soil could only be blown at wind speeds higher than 18 m/s. Although the data did not allow for statistical testing, wind-blown sand appeared to contain proportionally less fine soil particles than non-blown sand (Fig. 2).

Dry weights of plants grown in unsterilized soil were significantly lower than those grown in sterilized soil (Fig. 3). After the soil had been transported at a wind speed of 22m/s, the biomass production of *Ammophila arenaria* in unsterilized, wind-blown soil was significantly higher than that in unsterilized, non-blown soil (Fig.3). Also the growth of seedlings in sterilized, wind-blown soil was significantly lower than that in sterilized, non-blown soil.

The total number of fungal colonies in wind-blown soil did not differ from that in non-blown soil (Table 2). Numbers of *Acremonium* spp., *Fusarium culmorum*, and *Mortierella* spp. were significantly lower in soil that was blown. On the other hand, the number of *Phoma* spp. was higher in the wind-blown soil than in non-blown soil (Table 2). The numbers of *Fusarium culmorum*, the other species of *Fusarium* combined, *Penicillium* spp., and *Phoma* spp., as well as the total number of fungal colonies, were negatively correlated with particle size (Table 2). This indicates a decrease in Colony Forming Units (CFUs) as the soil particle size increases. This relationship could be expected since the particle area/ weight unit decreases with increasing particle size.

Directly after wind-driven transport, the numbers of plant-parasitic nematodes, dorylaimids and non-plant-feeders were reduced, compared to non-blown soil (Table 3). No nematodes could be detected in soil blown at 22 m/s (Table 3). After conducting the bioassay, all types of nematodes were isolated.

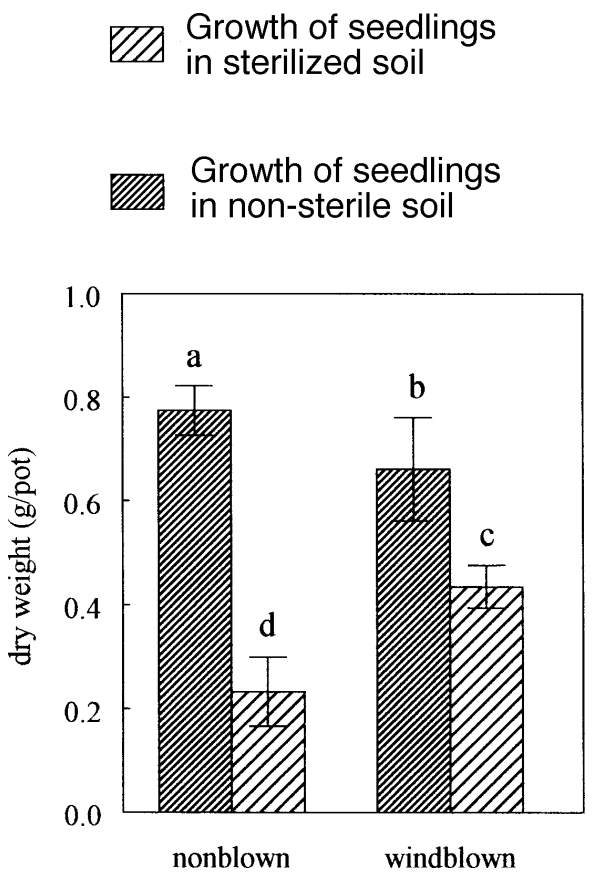

Fig. 3. Biomass production after six weeks of *Ammophila arenaria* seedlings planted in wind-blown or non-blown soil. Soil was blown in a wind tunnel at a wind speed of 22 m/s. The growth of the seedlings in sterilized soil (fine hatching) was compared to that of non-sterile soil (open hatching). Bars bearing different letters are significantly different at $P \leq 0.05$.

Table 2. Correlation between fungi (number of colony forming units per g dry soil) and treatment (wind-blown at 22 m/s and non-blown) particle size. WilcoxonÕs rank sum test was used for comparing the two treatments (P_W). For correlation between particle size distribution and fungi the Pearson rank correlation coefficient and its significance are presented. Only dominant fungal species were compared.

	Treatment	Particle size	
	P_W	Correlation	P
Acremonium spp.	< 0.001	Ð 0.26	0.114
Cladosporium spp.	0.333	0.05	0.410
Fusarium culmorum	<0.001	Ð0.42	0.021
other *Fusarium* spp.	0.259	Ð0.55	0.003
Mortierella spp.	0.014	Ð0.31	0.443
Mucor hiemalis	0.445	0.04	0.427
Penicillium spp.	0.112	Ð0.45	0.014
Phoma spp.	0.028	Ð0.48	0.009
Trichoderma harzianum	0.768	0.28	0.095
Total colonies	0.729	Ð0.50	0.006

Table 3. Nematodes (number per 100 ml soil) in non-blown and wind-blown (at 22 m/s) soil directly after being transported by wind (N= 2) and at harvest (N=6) of the pot-experiment. Significant differences between the numbers of nematodes of non-blown and wind-blown sand are indicated with * (Tukey test: $P < 0.05$).

	Non-blown	Wind-blown
Directly after wind transport		
Plant parasites	3.5	0
Dorylaimids	16.5	0
Non-plant-feeders	45	0
After pot experiment		
Plant parasites	3	1 *
Dorylaimids	34	0.3 *
Non-plant-feeders	143	130 *

Table 4. Numbers of nematodes five days after mechanical stirring of the soil (A) and after a pot-experiment (B) with this soil for eight weeks. The numbers are means of three replicates. The soil was stirred at speeds of 0 to 1500 rpm for 15 min. jv = juveniles. Significance of differences were only tested for the total number of plant parasites, Dorylaimidae, and non-plant-feeding nematodes and are marked with different letters at $P \leq 0.05$.

A	Rpm				
	0	300	600	900	1500
Pratylenchus spp.	1.8	0.5	0.7	0.6	0.6
Rotylenchus goodeyi	22.1	0.7	0.4	3.1	0.2
Filenchus spp.	0.5	0.2	0.5	0.2	0
Telotylenchus ventralis	1.2	0.6	0.5	0.4	0.1
Hemicriconemoides spp.	0.2	0	0	0	0
Heterodera spp. (jv)	14.8	13.7	18.4	14.4	13.3
Meloidogyne maritima (jv)	19.1	29.1	40.2	21.4	7.5
Heteroderidae (males)	1	1	0	0.5	0.2
Aphelenhus spp.	1.2	2.5	0.1	0.1	1.6
Plant parasites	60.8 a	45.9 ab	60.7 a	40.6 ab	22.1 b
Dorylaimidae	4.4 a	4.7 a	0.6 b	1 b	0.7 b
Non-plant-feeders	32.5 a	28.4 a	19.3 b	12.1 b	11.4 b

B	Rpm				
	0	300	600	900	1500
Pratylenchus spp.	0.1	0	0	0	0
Rotylenchus goodeyi	19.1	0.1	0.1	1.1	0.1
Helicotylenchus spp.	0.5	0.1	0	0.2	0.1
Filenchus spec.	0	0.1	0.1	0.2	0
Telotylenchus ventralis	0.1	0	0.1	0.4	0
Hemicriconemoides sp.	0.5	0	0	0	0
Heterodera spp. (jv)	0	0.6	0	0	0
Heteroderidae (males)	0.2	0.2	0.7	0.6	2.3
Aphelenhus spp.	0	0	0.5	0	0
Plant parasites	20.6 a	1.2 b	1.1 b	2.6 b	2.6 b
Dorylaimidae	1.7 ab	3.2 ab	4.1 a	1.9 ab	1.5 b
Non-plant-feeders	53.3 a	88.9 a	65.6 a	117.9 a	113.6 a

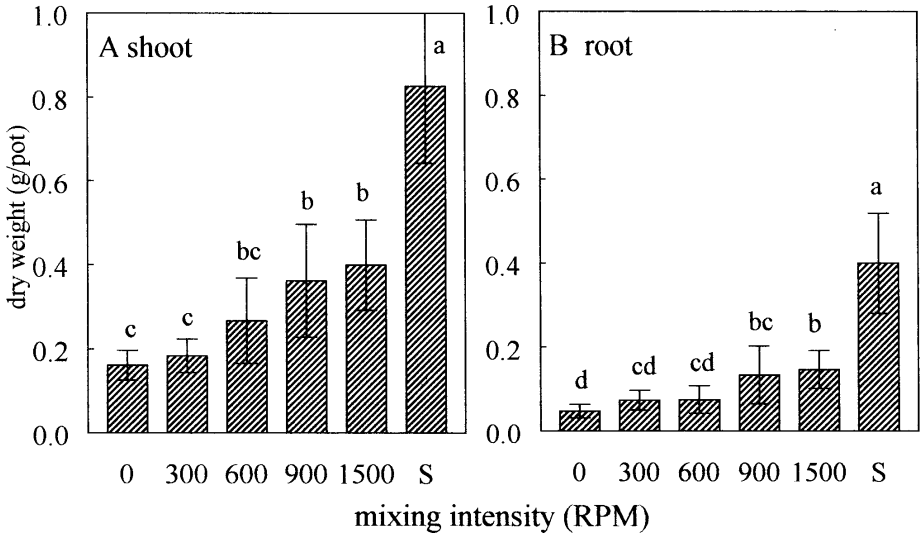

Fig. 4. Biomass production (g dry weight per pot) of shoots (A) and roots (B) of *Ammophila arenaria* seedlings after a growing period of eight weeks in soil previously stirred at different rpm (0, 300, 600, 900 or 1500) and control (non-stirred), sterilised soil (S). Bars bearing different letters indicate significant differences at $P \leq 0.05$.

Effects of scouring

After a growing period of eight weeks in soil stirred at a speed of minimally 900 rpm, shoot dry weights were significantly higher than the control (Fig.4A). The shoot dry weight of plants grown in sterilized soil was significantly higher than that of plants in any of the other treatments. The soil had to be stirred at 1500 rpm in order to obtain a significantly increased root production (Fig. 4B).

Increasing stirring intensities resulted in decreasing numbers of fungal propagules (Fig. 5). At least 900 rpm had to be applied in order to obtain a significant decrease in the number of fungal propagules as compared to non-mixed soil.

Numbers of dorylaimids, plant-feeding nematodes and saprobiotic nematodes had significantly decreased after soil had been stirred (Table 4). Most plant-parasitic nematodes decreased rapidly as the stirring intensity increased. However, the numbers of juveniles of *Heterodera* spec. and *Meloidogyne maritima* were not affected by stirring the soil. At harvest, roots in soil stirred at 600 rpm had higher numbers of cysts and rootknots than roots in soil stirred at 300 or 900 rpm and about ten times higher than in unscoured soil (data not shown). These cysts and rootknots were not yet full-grown, so that at harvest no new juveniles could be isolated (Table 4B). The fact that no juveniles could be isolated resulted in a significantly ($P < 0.05$) lower number of plant-parasitic nematodes at harvest than at the start of the experiment (Table 4; ANOVA not shown). The non-plant-feeding nematodes had increased significantly during the pot-experiment whereas the numbers of dorylaimids remained stable.

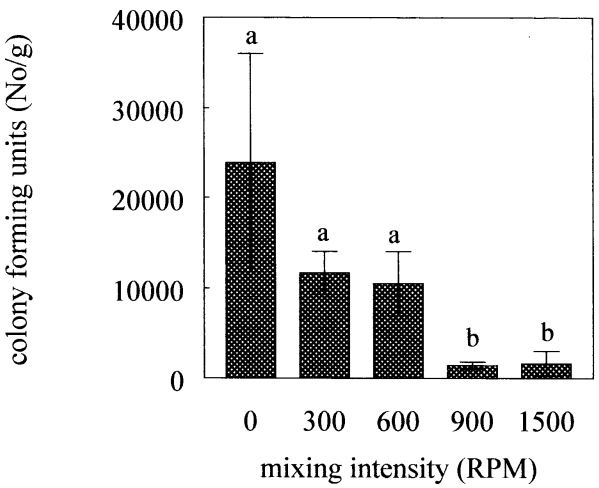

Fig. 5. Numbers of fungi (colony forming units per g dry soil) in soil stirred at different rpm values: 0, 300, 600, 900 and 1500. The numbers were assessed directly after stirring the soil. Bars bearing different letters indicate significant differences at $P < 0.05$.

Discussion

This study shows that aeolian transport of sand from the root zone of *Ammophila arenaria* may reduce the number of pathogenic soil organisms. Plants benefit from sand deposition particularly when the sand does not contain pathogens and parasites (de Rooij-van der Goes et al. 1995a, b). Rejuvenation of stands of *Ammophila* along the edges of blowouts where wind-blown sand accumulates may, therefore, be explained (at least in part) by the reduced inoculum pressure of plant-pathogenic organisms in the deposited soil.

In the blowout in the Goeree dunes, as well as in the wind tunnel, sand was mostly transported just a few cm above the soil surface. This type of movement implies heavy bouncing and saltation of soil particles (Bagnold 1954) and a resulting heavy scouring of sand particles. A stirring experiment partly simulated this type of sand movement and showed that scouring of soil particles probably crushed and destroyed free-living nematodes between the sand particles. Mechanical stirring of soil killed most plant parasites and dorylaimids. However, cyst nematodes (*Heterodera* spp.) and root-knot nematodes (*Meloidogyne maritima*) did not seem to be negatively affected. More Heteroderidae juveniles were able to infect the roots in stirred soil than in non-stirred soil.

As Eisenback & Griffin (1987) and Eisenback (1993) indicated, the more extensive infections could have been due to an absence of other parasites that inhibit successful infections. However, the increase in infection intensity did not result in growth inhibition of the test plants. *Rotylenchus goodeyi* was severely affected by stirring of the soil. A parasitic relationship between nematode infection and growth inhibition has not yet been established for this species. However, for another ectoparasitic species, *Telotylenchus ventralis*, such a relationship has been established: plant growth is strongly inhibited when this nematode species is added in high numbers (de Rooij-van der Goes 1995). A similar relationship may also be the case for *R. goodeyi*.

Unlike nematodes, fungi and bacteria were mainly transported attached to soil particles. Fungi are known to form small aggregates of sand particles (Forster & Nicolson 1981). Wind-driven sand movement was expected to disintegrate these aggregates and to rub off and destroy the fungal hyphae. Indeed, most aggregates were broken after sand had been blown within the blowouts, but the wind tunnel experiment showed no decrease in the total number of fungal propagules transported by wind. Only the numbers of *Fusarium culmorum*, *Acremonium* spp. and *Mortierella* spp. were reduced when soil was blown. As *F. culmorum* is associated with smaller particles, this fungus may also have been blown from the soil in suspension. The numbers of propagules of other fungi, however, were not correlated with particle size. Their reduction after wind-borne sand transport implied that they were most likely destroyed by scouring of sand grains. This mechanism certainly proved to reduce the numbers of fungal propagules in the stirring experiment. We may expect that plant growth in the scoured soil as compared to untreated soil will be enhanced due to a reduction in both the numbers of fungal propagules and plant-parasitic nematodes.

Apart from being affected by scouring, soil organisms may also be eliminated from the wind-blown sand by sifting out when sand is transported in suspension over long distances. In our experiments, the proportion of small-sized soil particles tended to decrease after soil was blown through the wind tunnel. This meant that a larger proportion of big particles was captured in the cotton bags than smaller particles. Also, sand deposited at the accumulation site of blowouts and on the seaward slope of coastal foredunes contained a larger proportion of large-sized sand particles than at the deflation site (P.D. Jungerius unpubl. data). The disappearance of small soil particles from the sand deposited along the edge of blowouts may imply that those nematodes and fungal propagules which are not attached to soil particles may easily be sifted out. The occurrence of transport of fungi by wind over large distances is well-known (Gregory 1961; Zadoks & Schein 1979); nematodes in anhydrobiotic state, in cysts or egg-masses can also be easily transported by wind (Orr & Newton 1971).

The reduced biomass of plants grown in wind-blown, sterilized soil compared to that in non-blown, sterilized soil may have been a side-effect of the larger soil particles. Movement by wind changes the texture of the soil. However, the growth reduction of plants (sterilized vs. unsterilized) in non-blown soil was still larger than in wind-blown soil.

In conclusion, the effects of scouring and elimination of small particles may both contribute to the reduction of soil organisms in sand originating from blowouts. Due to the process of wind-driven transport at the accretion site, sand which is relatively free of soil organisms is deposited upon the vegetation. Therefore, the vigorous response of declining *Ammophila arenaria* at a depositional lobe of a blowout (van Dieren 1934; Huiskes 1979; Disraeli 1984; Willis 1989; Baye 1990) can, at least partly, be explained by the elimination of soil-borne pathogens (de Rooij-van der Goes et al. 1995a).

Implications for coastal dune management

At sites with little or no sand accumulation, plants degenerate and bare patches within the vegetation may develop. In the absence of succeeding plant species, these exposed sites are vulnerable to wind erosion and therefore form a threat to the function of dunes as a natural sea wall. However, bare patches are frequently covered by algae and mosses (Pluis & De Winder 1990). As trampling causes breaking of these crusts, wind erosion can easily occur at such sites. Replanting *Ammophila arenaria* often fails as plants cannot establish due to the presence of harmful soil organisms.

In spite of the potential danger of an ineffective sand-fixing vegetation, wind erosion also proved to enhance the vigour of the plants as soil-borne organisms are killed during sand movement by wind. Therefore, serious consideration should be given to the reactivation of blowouts to rejuvenate declining stands in stabilized foredunes.

Until now it has been common practice to reshape and replant areas where blowouts became too large. By reshaping, root-zone sand is deposited in the centre of blowout resulting in poor establishment of the replanted culms. Based on the results of the experiments in this paper and previous work (de Rooij-van der Goes 1995; de Rooij-van der Goes et al. 1995a), it should be considered not to reshape the blowout but to replant *Ammophila arenaria* in the centre where soil-borne pathogens are nearly absent. As the side-walls becomes less exposed to wind-erosion, the blowout will stabilize. By further colonization through horizontal rhizomes, the whole blowout becomes vegetated. These rejuvenated stands, will maintain their value as a dynamic natural defence against the sea. Sand nourishment in the framework of the Ôdynamic preservationÕ (Hillen & Roelse 1995) of the Dutch dunes will also lead to rejuvenation of the dunes.

There are several possible measures to reactivate deteriorated stands of *Ammophila arenaria* such as mowing, ferilization and below-ground cutting (van der Putten & Peters 1995). Supply of fresh sand and subsequent action of wind-blown sand eliminating soil pathogens is another measure.

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