

Release from native root herbivores and biotic resistance by soil pathogens in a new habitat both affect the alien *Ammophila arenaria* in South Africa

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Abstract

The European dune pioneer *Ammophila arenaria* (marram grass) was introduced in the 1870's in South Africa and has ever since been used to stabilise Cape coastal dunes. At present the alien grass is still an important drift sand stabiliser. Recently, however, the use of *A. arenaria* has been criticized due to its foreign origin and the proven facts of invasiveness in other parts of the world. One of the major explanations of the success of introduced species in recipient communities is their release from natural enemies (Enemy Release Hypothesis - ERH). On the other hand, when exotic plant species fail to invade new habitats this has been related to biotic resistance from the native communities to be invaded (Biotic Resistance Hypothesis - BRH). In its area of origin *A. arenaria* dominates the fore dune plant community of mobile dunes, but it disappears naturally when dunes become stabilised mainly due to growth control by soil-borne pathogens. We examined ERH and BRH in relation to the invasiveness of the exotic fore dune grass *A. arenaria* in South Africa. The results from our study support both ERH and BRH in the case of soil pathogens of the introduced *A. arenaria* in South African dunes, indicating that ERH and BRH may be active simultaneously. Possibly a number of exotic plant species that does not become highly invasive, such as *A. arenaria* in South Africa, experience both ERH and BRH. The balance between enemy escape versus biotic resistance will determine the invasiveness of a species in a new habitat. In the case of *A. arenaria*, the generalist nematodes and the negative soil feedback apparently originate from the local grasses, whereas the dicots were less important in sharing potential pathogens. Our results further suggest that not only the local plant species diversity, but also the type of plant species present will determine the potential for biotic resistance. The biotic resistance against invasive plant species may depend on plant competition, but also on the presence of plant species that are hosts of potential soil pathogens that may negatively affect the invaders.

Keywords: Coastal fore dunes; Invasive plants; Plant-parasitic nematodes; Plant-soil feedback; Sand stabilisation.

Introduction

Over 80% of South Africa's 3 000km coastline is made up of sandy beaches and dunes, home to many endemic plant (and animal) species. Strong winds, high salt loads and sand movement restrict the number of species present in the fore dune vegetation to a few hardy 'pioneer' species on the frontal dunes (Tinley, 1985). The misuse and destruction of the (vegetated) dunes resulted in wind-driven movement of dunes inland, threatening adjacent property (DEAT, 2000). To prevent this 'unwelcome' sand movement, (rigid) structures are erected or the dunes are artificially stabilised with vegetation, often using alien sand-binding species (*e.g. Acacia cyclops*, *Ammophila arenaria*; Richardson *et al.*, 1997). In the view of disturbances that South African ecosystems experience through alien plant invasions (MacDonald *et al.*, 1986), the use of alien species for restoration and stabilisation purposes is highly questionable. The concern about *A. arenaria* is justified when seen against the background of the situation in North America and Australia, where the introduced grass is clearly invasive and has a major impact on indigenous dune vegetation and dune geomorphology (Heyligers, 1985; Wiedemann and Pickart, 1996). Presently *A. arenaria* occurs along ca.1500km of South African coastline only at the sites where it was introduced and research so far does not indicate that unaided spread of *A. arenaria* occurs (Hertling and Lubke, 1999). Where the introduced grass grows, it contentedly co-exists with the indigenous fore dune vegetation (Knevel, 2001). Hence, at present *A. arenaria* is considered to be non invasive in South Africa.

Why is *A. arenaria* not invasive in South Africa?

One reason could be the climatic factors as the South African sites where *A. arenaria* occurs, are either too dry or too hot (Peter, 2000) and are subjected to higher radiation, stronger winds and lack regular frost periods needed to enhance germination (Huiskes, 1979). In addition to this, the growth of the species in its area of origin is controlled by soil-borne pathogens. It is known that pathogens can alter particular life-history characteristics by inducing morphological and/or physiological changes in host plants, and as such can have a high impact on the structure of plant communities (*e.g. Van der Putten et al.*, 1993). The potential importance of soil-borne pathogens will, however, depend upon both the frequency of infection and the nature of pathogen effects on the host(s), relative to other biotic and abiotic features of the local environment (Clay and Van der Putten, 1999). This interaction of *A. arenaria* with soil-borne pathogens might give a powerful indication on why the species is not invasive in South Africa at present.

One of the main explanations of the success of introduced species in recipient communities is their release from specialized natural enemies (Keane and Crawley, 2002). The release from these natural enemies (*i.e.* herbivores, pathogens) enables exotic species to increase in abundance and distribution (Enemy Release Hypothesis (ERH); Keane and Crawley, 2002). It has been found that many exotic plant species have less specialist herbivores and pathogens than similar native plant species in the invaded ecosystems (*i.e.* Mitchell and Power, 2003), supporting the ERH. However, according to the tens rule of Williamson (1996) only a minor proportion of introduced alien species become invasive in their new habitat, and even species from the same genus (*e.g.*

Ammophila) can behave very differently in their entire range of new environments. For instance, in North America both *A. breviligulata* and *A. arenaria* were introduced, but only the latter created problems (Seabloom and Wiedemann, 1994). One clarification for why many species are unsuccessful in spreading in recipient communities is described by the biotic resistance hypothesis (BRH); Invasion of native communities by exotic species can be counteracted by competitive species, as well as by local pathogens and other enemies that may control the new species following introduction (Elton, 1958; Maron and Vilà, 2001).

The introduction of *A. arenaria* into South Africa from seeds may have allowed the plants to escape from their soil-borne pathogens, supporting ERH. On the other hand, even though the current impact of *A. arenaria* on the dune systems in South Africa is considerable, the grass is considered to be non-invasive at present (Hertling and Lubke, 1999). This opens possibilities for BRH to explain the situation within the South African dune system. In order to test ERH, *A. arenaria* seedlings^{NL} have been grown in sterilised soils from European dunes. To compare negative soil feedback from the native habitat in Europe and the new habitat in South Africa, non-sterilised soil from both Europe and South Africa has been added to the sterilised soil and *A. arenaria*^{SA} plants have been grown to study their response. The biomass production of the test plants has been used to compare the direction and magnitude of the soil feedback in native and newly colonised soils. In order to test BRH, *A. arenaria* has been grown in sterilised and non-sterilised soils from a number of South African dune plant species. The difference of biomass production between plants grown in sterilised and non-sterilised root zone soils from the different South African plant species has been used as an indicator of negative soil feedback, which points at potential biotic resistance due to soil pathogens present in the new habitat. It is expected that there will be a specific plant-parasitic nematode community around each individual plant species, with a better performance of the plants when grown on 'foreign' soil due to the escape from their own pathogen and parasite community.

Material and method

Field survey

Root zone soil samples of *A. arenaria* and several indigenous plant species were collected from three sites along the Cape coast. At the sample sites, transects running parallel to the coastline were selected for monospecific stands of each plant species and divided into 10 plots. Within each plot a minimum of three soil and root samples of 1kg and 20g, respectively, were randomly collected. For each plant species the soil samples from a plot were pooled and stored in plastic bags in a dark cold room (5°C) until usage (after Van der Putten and Peters, 1997).

Nematode extraction and identification

Nematodes in the soil were isolated from a sub-sample of 400ml from sample by means of elutriation (Van Bezooijen, 1997) and the nematodes in the roots were isolated by the funnel-spray method (Oostenbrink, 1960). After extraction the nematodes were counted, identified, and assigned to the feeding classes (phytophagous, saprophagous or

omnivorous). Only the phytophagous nematodes (also called root-feeding or plant-parasitic nematodes) were identified up to genus level. For detailed information see Knevel *et al.* (2004).

Transplantation experiments

Two transplantation tests were carried out with *A. arenaria* grown on (1) *A. arenaria* soil from two countries (SA and NL) and different sites within countries, and (2) soil from different species origin within South Africa. In the first transplantation experiment seedlings of *A. arenaria* (NL origin as no seed production in SA) were grown in sterilised dune soil that was inoculated with *A. arenaria* soil originating from five Dutch sample sites, and from seven South African sites. From each site at least three soil samples of 100g each were collected as described for the field survey. The roots were separated from the soil, cut into pieces and re-introduced into the soil as a source of inoculation. The soil-root mixture (270g) was homogenised with 720g sterilised sand (Gamma radiated) to increase the inoculate volume (after Van der Putten *et al.*, 1988). For each site origin five pots of 1.5 l were filled with inoculated soil (NS treatment) or with sterilised soil without inoculate (S treatment). Dutch seeds were used to grow seedlings (no seed production in SA) and per pot four uniform two-week old plants were planted (growth methods follow Van der Putten *et al.*, 1988) and placed in a greenhouse in a completely randomised design under $20\pm 2^{\circ}\text{C}$ and a photo-period of 12 hours.

During the experiment the soil moisture was maintained at 10% by adding demineralised water every three to seven days. To counteract the nutrient release due to sterilisation (Troelstra *et al.* 2001) and to avoid nutrient deficiency during growth, a full-strength Hoagland nutrient solution was added on day 1 of the experiment, and subsequent once every week. After six weeks, the plants were harvested and roots were separated from the shoots. Total biomass, root:shoot ratio and relative production (NS biomass/S biomass) was determined. For detailed method information see Knevel *et al.* (2004).

In the second transplantation experiment *A. arenaria* (SA origin) was grown in non-sterile and sterilised root zone soil that originated from South African *A. arenaria* and the indigenous species *Arctotheca populifolia* (Asteraceae), *Ipomoea pes-caprae* (Convolvulaceae), *Ehrharta villosa* (Poaceae) and *Sporobolus virginicus* (Poaceae). Five samples of 20kg each were collected from monospecific stands of each species and treated as described above. Half of the homogenised soil-root mixture was autoclaved and of each origin five pots were filled with 1.5 l of non-sterile (NS) or sterilised (S) soil. As in South Africa no seeds were produced by *A. arenaria*, the plants were obtained from surface sterilised stem pieces that were pre-grown in sterilised soil. Per pot four uniform two-week old plants of *A. arenaria* were planted and treated as described above. Due to a fungal infection, that did not affect the other pots, the plants growing on *A. arenaria* soil did unfortunately not survive and were therefore excluded from further analysis.

Results

For all examined species, omnivorous, saprophagous and phytophagous nematodes were found but the densities and number of nematode genera found of three different feeding classes differed greatly between the species sampled (Table I). The density of

phytophagous (soil + root) and saprophagous nematodes (soil) was highest for *I. pes-caprae* ($P < 0.01$; Table I), whereas low densities were observed for *A. arenaria* (soil + root), *S. virginicus* (soil), *A. populifolia* (soil) and *E. villosa* (root) (Table I). In the root the highest saprophagous densities were found for *A. populifolia* and *A. arenaria* ($P < 0.01$; Table I). No significant differences were observed for omnivore nematodes ($P > 0.05$, Table I).

Table I. Mean nematode densities found in the soil (numbers per 400 ml soil, $n=10$) and root (numbers per gram dry root, $n=3$) given per feeding class for *A. arenaria*^{SA}, and four indigenous species (grass species marked with #). Any soil or root value within a feeding type with the same letter does not differ significantly. Contrasts obtained by Newman-Keuls after analysis by Kruskal-Wallis. Level of significance: ** = $P < 0.01$, *** = $P < 0.001$, ns = not significant, - = no data available

Species	Feeding class					
	Phytophagues		Saprophagues		Omnivores	
	Soil	Root	Soil	Root	Soil	Root
<i>A. arenaria</i> #	74.9 b	51.5 b	383.3 c	518.0 a	40	0
<i>E. villosa</i> #	163.3 a	842.2 a	366.7 c	237.3 ab	35	0
<i>S. virginicus</i> #	55.8 b	946.9 a	392.9 c	-	59.1	-
<i>A. populifolia</i>	32.5 b	35.3 b	666.7 b	547.8 a	36.7	0
<i>I. pes-caprae</i>	335.0 a	1092.9 a	929.2 a	188.4 b	82.5	0
<i>P</i> - value	***	***	**	**	ns	ns

In total, two endoparasitic nematode genera were present in the South African dune samples; *Pratylenchus* and *Meloidogyne*. However these never occurred in the same plant species at the same time. The species *E. villosa*, *S. virginicus*, and *I. pes-caprae* showed a high density for the endoparasitic nematodes (data not shown). *Pratylenchus* also occurred in stands of *A. arenaria*, but in relatively low densities, whereas no endoparasitic nematodes were found in the roots of *A. populifolia*. In spite of the lower densities of nematodes in the root zone of *A. arenaria* in South African samples, the total number of nematode taxa in the root zone of this introduced plant species was relatively high and showed the closest resemblance to the communities of the grasses *E. villosa* and *Elymus distichus* (Table II). The similarity of nematode genera between South African and Dutch *A. arenaria* populations ranged from 33-56% (Table II). Between the indigenous species and South African *A. arenaria* this ranged from 22-78% (Table II). As a consequence, monospecific *A. arenaria* stand from South Africa generally have more root-feeding nematode species in common with South African fore dune grasses, than with stands of *A. arenaria* in the Netherlands. This suggests that local root-feeding nematodes in South African dunes had used the introduced grass as an alternative host plant, rather than that the exotic plant species had introduced its own root-feeding nematode community. Also two sedimentary endoparasitic nematodes genera (*Heterodera* and *Meloidogyne*), were absent from South African *A. arenaria*, while these are common in the Netherlands (data not shown). There was only one single observation of a sedentary endoparasite for *A. arenaria*. However, this observation could not be confirmed in subsequent sampling expeditions. Therefore, the root zone of *A. arenaria*

in its new territories predominantly consists of nematodes that are usually considered as generalist root feeding nematodes.

Table II. Presence and absence of plant-parasitic nematode genera found in the rhizosphere of *A. arenaria* and indigenous dune pioneers. Within *A. arenaria* samples from the Netherlands (NL – Oostvoorne and Haringvliet; data originating from Van der Putten and Peters (1997)) are compared with different sites in South Africa (SA). Between the species *A. arenaria* is compared with seven indigenous fore dune species of South Africa (grass species are marked with *)

Sites/species	No. genera/feeding type				Similarity (%)	
	Endo parasitic	Semi-endo parasitic	Ecto parasitic	Total	with NL	with SA
Within <i>A. arenaria</i> :						
Oostvoorne/Haringvliet ^{NL}	3	1	5	9	-	-
Koeberg ^{SA}	1	0	5	6	33%	-
Tableview ^{SA}	1	0	5	6	33%	-
Kleinmond ^{SA}	1	1	7	9	56%	-
Die mond ^{SA}	1	0	6	7	33%	-
Klein brakrivier ^{SA}	1	1	5	7	44%	-
Sedgefield ^{SA}	2 ¹	1	5	8	44%	-
Blue water Bay ^{SA}	1	1	8	10	56%	-
Kleinemonde ^{SA}	1	1	3	5	33%	-
Between species:						
<i>A. arenaria</i> ^{SA}	1	1	7	9	-	-
<i>E. distichus</i> * ²	1	0	6	7	-	78
<i>E. villosa</i> *	1	1	6	8	-	78
<i>T. decumbens</i> ²	1	0	4	5	-	56
<i>A. populifolia</i>	0	0	4	4	-	33
<i>I. pes-caprae</i>	1	1	3	5	-	33
<i>S. plumieri</i> ²	1	0	2	3	-	22
<i>S. virginicus</i> *	1	1	2	4	-	22

¹ Second endoparasitic genus is from a single observation.

² Full species name: *Elymus distichus* (Poaceae), *Tetragonia decumbens* (Aizoaceae), and *Scaevola plumieri* (Goodeniaceae).

Transplantation experiments

When grown in non-sterilised Dutch (NL) and South African (SA) *A. arenaria* soil, at eight of the 12 sites the relative production was lower than the control (ANOVA, $P < 0.01$; Table III). In 3/5 of the NL sites *A. arenaria* produced less than half of the amount of biomass produced in sterilised soils compared to the control, whereas in the

SA dune soils a considerably smaller proportion (1/7) of sites showed a similar growth reduction (Table III). This demonstrates that the *A. arenaria* seedlings experienced considerably less negative soil feedback in its new habitat compared to its original habitat, which supports the ERH. On the other hand the 5/7 of the SA sites showed a lower RP compared to the control, showing that *A. arenaria* is indeed able to develop a negative soil feedback in its new habitat, providing supports for the BRH. Between the countries no overall significant difference in RP between the sites was found (Kruskal-Wallis, $P > 0.05$).

Table III. Mean relative production (RP = NS total biomass/S total biomass) (n=5) of *A. arenaria* plants grown on soil, originating from the Netherlands (NL) and South Africa (SA). Contrasts obtained by Tukey after analysis by one-way ANOVA. Level of significance: *** - $P < 0.001$

Sample site	RP	(±SE)	Sample site	RP	(±SE)
Control	0.95	(0.232) a ***	Chemfos ^{SA}	0.43	(0.185) d
			Die mond ^{SA}	0.85	(0.256) ab
Oostvoorne 1 ^{NL}	0.47	(0.132) cd	Kleinbrakrivier ^{SA}	0.80	(0.045) ab
Oostvoorne 2 ^{NL}	0.46	(0.131) cd	Koeberg ^{SA}	0.72	(0.040) b
Oostvoorne 3 ^{NL}	0.48	(0.206) cd	Milnerton ^{SA}	0.73	(0.127) b
Haringvliet 1 ^{NL}	0.78	(0.312) ab	Sedgefield ^{SA}	0.65	(0.113) bc
Haringvliet 2 ^{NL}	0.84	(0.336) ab	Stilbaai ^{SA}	0.66	(0.329) bc

When grown in foreign soil of native species, only the sterilisation of *S. virginicus* soil significantly enhanced biomass production, whereas no such effects occurred in the other three soils origins (ANOVA, $P < 0.001$; Fig. 1a). Subsequently, the plants grown in sterilised soil of *S. virginicus* showed the significant highest root:shoot ratio and a lower relative production ($P < 0.001$; Fig. 1b, c). Plants grown in non-sterilised soil from *I. pes-caprae* had the least growth reduction compared to the plants in the sterilised soil (Kruskal-Wallis, $P < 0.05$; Fig. 1a). These results show that the four South African fore dune plant species differed in their soil feedback to *A. arenaria*. While the soil feedback of most plant species supports ERH, the feedback from *S. virginicus* soil demonstrates that this plant species may contribute to BRH against *A. arenaria*, through negative feedback from the soil community.

Discussion and conclusion

In our study, we could confirm that the transfer of *A. arenaria* to South Africa has enabled the escape from endoparasitic nematode species that occur in their native habitat and which are supposed to be involved in the control of abundance of *A. arenaria* in stabilised dunes in the native habitat (Van der Putten and Van der Stoel, 1998). The root-feeding nematode community of *A. arenaria* in South Africa consisted mainly of rather generalist nematodes and was more similar to some local dune species, than to the community of its native European region. The nematode data found for *A. arenaria* in South Africa supports ERH when focussing on root-feeding nematodes. These results are similar to those reported in a review on aboveground herbivores and pathogens (Mitchell and Power, 2003). On the other hand most specialist nematodes are less harmful than

generalists and based on studies with root-feeding nematodes from Europe, it seems that the numbers of generalist root-feeding nematodes in the South African dunes might not be high enough to cause substantial growth reduction to *A. arenaria* (De Rooij-Van der Goes 1995). Other soil pathogens (*e.g.* pathogenic fungi) may be involved in the negative soil feedback (*i.e.* Van der Putten *et al.*, 1993).

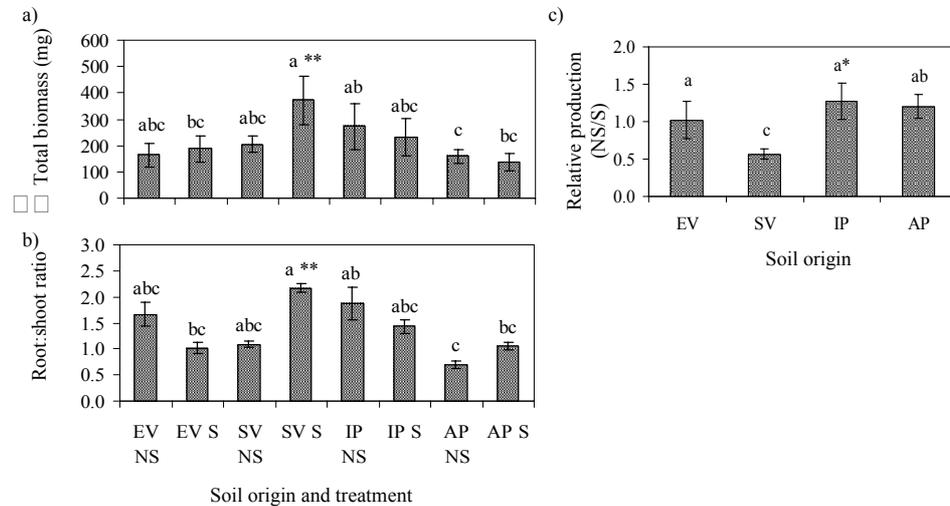


Fig. 1. Total biomass (a), root:shoot ratio (b) and relative production (c) of *A. arenaria* grown on the following soil origin and treatments: non-sterile (NS) and sterile (S) soil of *E. villosa* (EV), *S. virginicus* (SV), *I. pes-caprae* (IP), and *A. populifolia* (AP). Contrast obtained by Tukey after analysis by one-way ANOVA, except for relative production where contrasts obtained by Newman Keuls after analysis by Kruskal-Wallis. Level of significance: * $P < 0.05$, ** $P < 0.01$.

In SA *A. arenaria* soil the seedling growth was less reduced than in root zone soil from Dutch stands where the used seeds were collected from. The use of Dutch seeds may have underestimated the negative soil feedback in SA (*i.e.* local populations more susceptible to soil pathogens of their parents), but previous tests did not confirm such reduced impacts (Van der Putten and Troelstra, 1990), so that this possibility is not very likely. The less negative soil feedback in SA soil are in the range of effects measured in beach sand (Van der Stoel *et al.*, 2002), supporting ERH. The occurrence of a substantial negative soil feedback in some SA *A. arenaria* sites shows, however, that there is pathogenic activity in the stands, supporting BRH. This activity is probably mainly due to generalist root-feeding nematodes. It should be noted that other pathogenic factors may be involved in these processes (De Rooij-Van der Goes, 1995). The elucidation of the organisms that may have caused the growth reduction in the SA soils may be very complicated (De Rooij-Van der Goes, 1995), therefore soil feedback trials with other plant species were used in order to trace the potential soil pathogens source. When grown in soil from indigenous species, only the soil from the grass *S. virginicus* had a negative effect on growth of *A. arenaria*. The other plant species had a more neutral feedback, but no positive soil feedback was observed. These results support the BRH, since

the soil pathogens of one local grass species may be able to cause growth reduction to the exotic grass. At the sampled sites the cover and abundance of *A. arenaria*, *S. virginicus* and the other sampled species differs per site, but none of the species was dominant, but sheared a co-dominance with other species. In general the species form some scattered patches of higher abundance over the fore dune area, intermingled with other species, more so than a closed dense vegetation structure (Knevel, 2001).

The results do not support the suggestion that symbiotic arbuscular mycorrhizal (AM) fungi may have provided an advantage for SA *A. arenaria* (Callaway *et al.*, 2003). However, the effects of AM fungi may have been obscured by the addition of nutrients, which were added in order to avoid interference by a possible nutrient flush (Troelstra *et al.*, 2001).

In conclusion, the results from our study support both ERH and BRH in the case of soil pathogens of the introduced exotic dune grass *A. arenaria* in South African dunes. Biotic resistance against invasive plant species may depend on plant competition, but also on the presence of plant species that are hosts of potential soil pathogens that may negatively affect the invaders. The vigour and success of aliens in areas where they have been introduced has, besides release from natural phytophagous enemies, often have been attributed to more favourable environments. Perhaps the limited invasive capacity of *A. arenaria* in South African dunes is also limited by the combination of rainfall/temperature, perhaps in combination with pathogen effects found, making the South African coast at present unsuitable for the species to be invasive. The use of *A. arenaria* should nevertheless be restricted as the grass shows many invader traits and future climatic changes might favour invasiveness.

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