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Assessing the potential for biological invasion — the case of *Ammophila arenaria* in South Africa

U.M. Hertling* and R.A. Lubke*†

Many plants, especially woody species, introduced into South Africa for ornamental or commercial purposes, have become invasive in a number of habitats. Because of the risk of an invasion of coastal dunes by yet another species, the European dune grass *Ammophila arenaria*, used as a dune stabilizer, is assessed using lists of attributes of invasive species and invasible ecosystems. It is impossible to predict plant invasions, but both invasive species as well as invaded ecosystems are often characterized by certain attributes which facilitate invasions. Many of the species attributes connected with invasion appear to apply to *A. arenaria*. Above all, the grass is characterized by ecological tolerance and vigorous rhizomatous reproduction. An important site attribute connected with invasion is an evolutionary history with isolation patterns, which applies to the South African Cape coast. We conclude also on the basis of the overseas experience, that the potential for *A. arenaria* to become invasive needs urgent investigation in the South African context.

South Africa has a long history of alien plant invasion and much work has been done on the influence of invasive plants on the indigenous flora and vegetation[1,2] and the control of invasive plant species.[3] Many of these plant invaders have been introduced from Australia and South America, where the climate and habitats are similar.[1] A recent summary of alien plant invasions by Richardson *et al.*[1] provides a categorization of the invasiveness of many species and indicates the seriousness of the problem in South Africa (Table 1). Many individual studies of the biology of these alien species have been made in South Africa, for example *Pinus in mountain fynbos*[4] or jointed cactus in the Eastern Cape.[5] Biological control agents have also formed a focus of research, some of which have been released and are at least controlling the more extensive spread of some alien species.[1,6]

The European dune pioneer *Ammophila arenaria* (L.) Link (marram grass) was introduced to South Africa in the 1870s in an attempt to stabilize large driftsands in the vicinity of Cape Town.[7] It is still the most frequently used plant in the numerous dune stabilization projects along the Cape coast[8] (Fig. 1 A). In view of the drastic disturbances that South African ecosystems experience through alien plant invasions,[1,2,3,6] the wisdom of planting any alien species with the potential for invasion is highly questionable. *Ammophila arenaria* presently occurs along about 1500 km of South African coastline between Langebaan on the arid west coast and Gonubie in the subtropical, humid Eastern Cape.[9]

Concern about *A. arenaria* takes account of the situation in North America (Fig. 1 B), where the grass is clearly invasive and has a major impact on natural dune plant communities: not only does it cause the decline or even elimination of indigenous dune plants and their communities,[10–16] it also induces changes in dune topography.[11,17] Furthermore, it spreads rapidly even on more stable inland dunes[18,19] by means of sexual as well as vegetative reproduction.[20,21] Its competitive superiority over indigenous dune plant species is ensured by physiological advantages like efficient nitrogen use in photosynthesis and high resource allocation flexibility.[22,23] Adverse impacts of *A. arenaria* on dune biota and dune geomorphology have also been reported in Australia[24–26] and in New Zealand.[27–30] It is therefore a matter of urgency to establish whether *A. arenaria* is, or has the potential to become, an invasive plant species in South Africa. In pursuit of this aim, this paper makes use of lists of attributes that have been found to characterize both invader plants as well as invasible ecosystems.

*Department of Botany, Rhodes University, Grahamstown, 6140 South Africa.
†Author for correspondence. E-mail: borl@rhobot.ru.ac.za

Theories and definitions

Although the terms 'invader species' and 'invasion' have been dealt with extensively in the literature, there is still much ambiguity surrounding them. Most authors agree that a plant or animal species new to a territory can be termed invasive when it not only establishes a self-sustaining population in the host territory, but also spreads successfully from its point of arrival.[6] This definition does not address the mode of transport or the distance covered by the species from its home territory to the new territory. Invasion can therefore be studied at various scales of space and time.[31] In the case of plants, the newcomer plant can belong to the same ecosystem as the resident plants and move only a few kilometres or even metres from its place of introduction. For example, it might have arrived from a different successional stage, in which case the 'invasion' is merely one step in the natural succession of the ecosystem. The newcomer can also belong to a different ecosystem within the same region, or to a different region within the same biogeographical area. Lastly, it might have arrived from a different biogeographical area altogether, even thousands of kilometres distant..

In an attempt to make the concept more succinct, invasion can be defined as 'the entering of a species into a territory in which it has never before occurred, followed by the extension of the range of that species'.[32] An invader species must therefore have evolved in a different biogeographical area from the one that it invades, which excludes evolutionary developed processes such as succession or colonization by indigenous weeds. Another restriction is put forward by defining an invader species as 'a foreign taxon that enters an established ecosystem and contaminates it'[33] or that enters 'relatively intact vegetation and strongly dominates or even displaces it altogether'.[34]

To evaluate the possible negative influence of *A. arenaria* in South Africa, we will use the more restrictive definitions of invasion. We define invasion as 'the entering of a species into a territory in which it has never before occurred, followed by the unaided extension of the range of that species and the possible ecological disturbance of the host territory'.

The history of the introduction and use of *A. arenaria* in the stabilization of dunes in the Cape

Marram grass was first introduced to South Africa in 1876 as seed from Lincolnshire, England. In 1892 a much larger amount of seed came from northern France. In both cases, germination was low, but seedlings were grown into plants in Cape Town

Table 1. List of some terrestrial invasive plant species with an assessment of their impact (source refs 1–3).

Invasive plant species	Family	Origin	Biome or habitat° invaded	Undesirable characteristics+	Invasive potential or severity of impact*
Acacia cyclops (rooikrans)	Fabaceae	Australia	fy, fo, sa	c, r, t	10
Acacia longifolia (long-leaved wattle)	Fabaceae	Australia	fy, sa	c, r, t	7
A mearnsii (black wattle)	Fabaceae	Australia	gr, fy, fo, sa	c, r, t	10
Bidens bipinnata (blackjack)	Asteraceae	Europe/Asia	sa, gr	c, con	2
Casuarina equisetifolia (Australian pine)	Casuarinaceae	Uncertain (Pantropical)	fo, sa	c, r	1
Cestrum laevigatum (inkberry)	Solonaceae	South America	fo	c, r, p	5
Chenopodium album (white goosefoot)	Chenopodiaceae	Europe/Asia	sa, gr	c	2
Chromolaena odorata (triffid/turps weed)	Asteraceae	South America, West Indies	fo, sa	c, r, t	10
Cirsium vulgare (Scotch thistle)	Asteraceae	Europe/Asia	ka, gr, sa, fo	c, r, con	3
Datura stramonium (stinkblaar)	Solonaceae	South/Central America	sa, ka, gr, fo	c, r, con, p	6
Eucalyptus grandis (blue gum)	Myrtaceae	Australia	gr, fy, sa, fo	c, r, t	8
Hakea sericea (silky Hakea)	Proteaceae	Australia	fy, fo	c, r, t, con	5
Lantana camara (common Lantana)	Verbenaceae	South/Central America	fo, sa, fy, gr	c, r, t, con, p	10
Opuntia aurantiaca (jointed cactus)	Cactaceae	South America	ka, sa	c, con	8
Opuntia ficus-indica (prickly-pear)	Cactaceae	Central America	sa, ka, gr, fo, fy	c, r, t, con	6
Pennisetum clandestinum (kikuyu grass)	Poaceae	Africa	fy, sa, gr, ka	c, r	5
Pinus pinaster (cluster pine)	Pinaceae	Mediterranean Basin	fy, fo, sa	c, r, t	7
Sesbania punicea (red Sesbania)	Fabaceae	South America	sa, fo, fy, gr	c, r, p	4
Solanum mauritianum (bug weed)	Solanaceae	South America	fo, gr, sa, fy	c, r, t, p	8
Tagetes minuta (kakiebos)	Asteraceae	South America	sa, gr, ka, fo	c, r, con	6
Xanthium spinosum (spiny cocklebur)	Asteraceae	South America	ka, sa, gr	c, r, con	3

°Biome: fy, fynbos; fo, forest; gr, grassland; ka, karoo; sa, savanna.
+Undesirable characteristics: c, competitive; r, replaces indigenous vegetation; t, transforms landscapes; con, contaminant of wood, seeds, etc or thorny; p, poisonous.
*Severity of impact: 1, minor problem, but has potential to increase in the next few decades; 2–4, moderately invasive; 5, successfully invaded, difficult to control; 6–9, invaders almost impossible to control; 10, most extreme invader, likely to invade thousands of hectares of indigenous vegetation.

nurseries. The planting of bundles of *A. arenaria* culms became the most important stabilization technique along the Cape coast in the last century, particularly since concern about the previously favoured, but highly invasive Australian acacias was raised in the 1930s. Large-scale stabilization areas with *A. arenaria* were created along the Cape coast between Saldanha on the west coast and Gonubie near East London. Although the stabilization of dunes in itself has been questioned in South Africa since the 1980s and guidelines of the Council for the Environment suggest their avoidance wherever possible, the grass is still planted frequently. Its modern distribution from the semi-arid west coast to the subtropical shores of the Eastern Cape extends through various climatic zones. *Ammophila arenaria* is widespread along the Cape coast, but it occurs at most sites because of its prior planting. Although historical data are missing for some areas, there is no indication of its unaided spread.

Assessing invasion potential

Not every alien species turns out to be invasive. Only 1–3% of all introduced species (including imported, but contained species) in Britain and Germany are able to establish self-sustaining populations in the new territory, and less than 1% will spread and cause problems.[36] According to the 'tens rule', that is, 10% of introduced species (excluding imported, but contained species) become established, and 10% of those established become pests.[37] Sometimes, species from the same genus behave very differently in a new environment, one being highly invasive and another causing no problems:[31] both *Ammophila arenaria* and *Ammophila breviligulata* were introduced to the

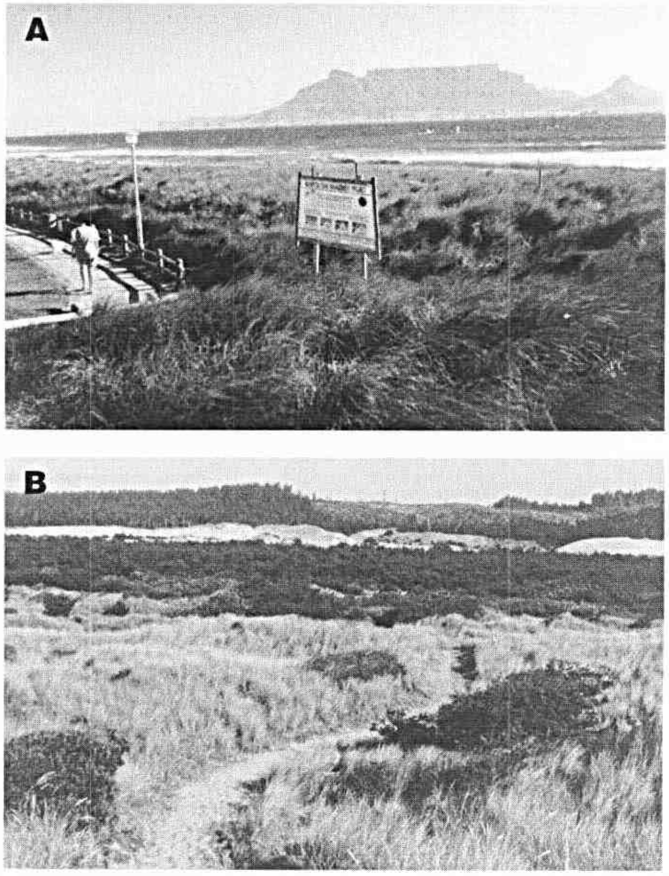

Fig. 1. A, stabilization site featuring *A. arenaria* at Tableview, north of Cape Town (January 1996); **B**, view from foredune looking inland across deflation plain covered with *A. arenaria* and *Pinus contorta* at Carter Lake, south of Florence, Oregon (August 1996).

North American west coast, but only the former creates an ecological imbalance.[38] What then are the prerequisites of invasion? This was the central issue of an international project on the 'Ecology of Biological Invasions', launched in 1982 by the Scientific Committee on Problems of the Environment (SCOPE). It was followed by a number of regional workshops. A global perspective is given by Drake *et al.*[39]

Not only must a potential invader species carry traits enhancing its potential invasiveness, it also has to meet an invasible system. Furthermore, extrinsic factors such as human actions, historical opportunity or even pure chance must be favourable.[4] Invasion is such a complex ecological process that pessimism regarding its predictability is expressed in most publications.[40] It is suggested that each particular case of biological invasion represents a unique event.[41] There is so much contingency involved in biological invasions that no two situations are alike and the study of invasion is required by some to be entirely a case-by-case analysis.[33]

Attempts have been made at developing mathematical models of invasion to enhance predictability.[42] Crawley's[43] model equates the invasiveness of a plant species with its intrinsic rate of increase in the host territory, from which functions relating to biotic barriers such as competition, enemies or the lack of mutualists must then be subtracted. An examination of the use of mathematical models in relation to the problem of biological invasions shows that they do not make reliable predictions in individual cases, but can be helpful in providing explanations of why an invasion has or has not happened.[37] Simulation models can lead to some qualitative generalizations about invasions that are at least not in contradiction with existing field data.[44]

Another approach to predicting invasions is the collection of features of proven invader species in checklist format. Baker's[45] list of the characteristics of 'the ideal weed' started this trend, which was followed by many other authors (e.g., refs 31, 32, 34, 46). Attributes of invader plants and invaded habitats are collected and summarized from experimental studies of invasions (e.g., refs 41, 47–49). As with mathematical models, the predictive value of such lists is often limited. Broad generalizations about attributes leading to biological invasions rely too heavily on retrospective analyses of past — successful — invasion events, excluding observations of communities that have not been invaded.[50] This inhibits the development of a coherent theory about the likelihood of invasions.

The assessment of a potential for invasion with lists of attributes is recommended before starting lengthy observational or experimental work on alien species, and particularly before a premature, public outcry about possible detrimental effects of an alien that may have many useful traits. We suggest the application of such lists only in well-determined cases. Richardson *et al.*[51] and Rejmánek and Richardson[52] use selected life history attributes of plant taxa to predict their invasiveness quantitatively. Richardson *et al.*[4] collected factors that determine the likelihood of an introduced species of the genus *Pinus* to become invasive in the southern hemisphere and of a recipient habitat to become invaded by pines. These studies show that a case-specific approach in assessing the risk of invasion can lead to viable information as well as providing the means for setting meaningful management priorities. Tables 1 and 2 list features that facilitate plant invasions, describing attributes of both possible invader plants as well as sites prone to become invaded. These checklists may be usefully applied to our case of *A. arenaria* and the dunes of the South African Cape coast.

Ammophila arenaria in South Africa — a possible invader?

Does *A. arenaria* have features that warn us of its potential invasiveness? Are the dunes of the South African Cape coast prone to invasion by this species? We will review the literature on its biology and on physical and biotic properties of the Cape coast with regard to these questions. Of particular importance are those studies on *A. arenaria* in North America, which not only describe the harmful impact of the grass but offer explanations for its success. The examination follows closely the lists of Tables 2 and 3. Results are reflected in both tables as positive (+), negative (–) or unknown (?). It is important to note that the lists are not aimed at predicting invasions but at warning of potential invasion. The likelihood for invasion cannot be measured but is indicated through a qualitative analysis of features of the respective species and ecosystem.

Attributes of *A. arenaria* that make it potentially invasive (Table 2)

Attributes related to ecology and physiology

Ecological tolerance

High acclimation potential and broad physiological response breadth (+). *Ammophila arenaria* occurs naturally from the Faeroe Islands to the shores of the Black Sea and is characterized by its tolerance of extreme temperature fluctuations and drought.[53] Essential for its vigour is a substratum of mobile sand with low organic matter content and a salt content of less than 1%, a condition that can be found all over the world as well as along the South African coast.

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Table 2. Species attributes connected with invasion (adapted and modified from refs 26, 27). (+) applies, (–) does not apply to *A. arenaria*; (?) not known whether applicable (see text).

Attributes related to ecology and physiology	
Ecological tolerance:	high acclimation potential and broad physiological response breadth (+) high resource allocation flexibility (+) non-specialized germination patterns (–)
Large biomass:	heavy seed (–) with high longevity (+) long growth period (+) high relative growth rate (?)
Specific phenology (avoidance of competition):	dormancy (+) unusual photosynthetic pathway (–)
Attributes related to demography	
Sexual reproduction:	early reproductive maturity (–) non-specialized seed production patterns (+) high resource allocation to seed production (?) long dispersal of seed in space (–) long dispersal of seed in time (+)
Vegetative reproduction:	rhizomatous or stoloniferous reproduction (+)
Attributes related to genetics	
Plasticity:	genetic variability (?) polyploidy (+) non-specialized pollination patterns (+)
Specific mating system:	autogamy (?) apomixis: vegetative apomixis (+) and/or agamospermy (–)

To avoid water loss, the leaves of *A. arenaria* bear stomata only in furrows between the hairy ribs of their adaxial surface; furthermore, leaves are tightly inrolled under hot and dry conditions. In response to water stress, *A. arenaria* was observed to develop stress metabolites such as proline and betaine; they enhance the heat stability of enzymes which otherwise suffer severely from increased heat because of stomatal closure under water stress.[54] No studies have been carried out on the photo-responses of the grass. However, on the west coast of North America, *A. arenaria* produces taller, denser and more vertically orientated leaves than *Leymus mollis* (formerly *Elymus mollis*, an indigenous American dune grass), which permits a more efficient use of direct and diffuse radiation.[55]

High resource allocation flexibility (+). Studies on the mechanisms of nitrate accumulation and reduction in *A. arenaria* prove that the grass responds swiftly to a change in soil water level, reducing nitrate in humid periods and storing it in dry.[56] A comparison of resource allocation techniques of *A. arenaria* and *Elymus mollis* demonstrates that the former partitions a larger fraction of its blade nitrogen pool into active photosynthetic enzymes than does *L. mollis*.[22] The efficient nitrogen use in photosynthesis appears to contribute to *A. arenaria*'s significantly higher long-term carbon gain. Furthermore, *A. arenaria* contributes a higher allocation of dry matter and nitrogen to live blades than *E. mollis*, thus exhibiting greater above-ground productivity.[23]

Non-specialized germination patterns (–). Seed germination of *A. arenaria* requires a highly fluctuating temperature regime, which is usually found on mobile dunes. Furthermore, a cold period of one to several months, as is the case on European dunes in winter, enhances germination.[53,57] However, temperature stratification under laboratory conditions does not significantly affect germination of American *A. arenaria* seed.[21]

Large biomass

Heavy seed (–) *with high longevity* (+). *Ammophila arenaria* seeds are small, weighing less than seeds of other European dune grasses[58,59] and various South African dune plants.[60,61] Seed longevity, on the other hand, appears to be high in *A. arenaria*, as it was found that storage of seed tends to improve germination.[53]

Long growth period (+). Shoots of *A. arenaria* in Europe grow mostly between April and September, but slow growth of tillers and individual leaves is still recorded in autumn and winter.[53] Flowers are initiated in autumn and appear the following spring. *Ammophila arenaria* is both a hemicryptophyte and a geophyte. Buds are found all year round, and slow vegetative growth also occurs during winter.

High relative growth rate (?). Little is known about the components of the relative growth rate of *A. arenaria*, namely its net assimilation rate (photosynthesis, respiration), leaf weight ratio (carbon partitioning) and specific leaf weight. However, American studies[22,23] prove not only a more efficient nitrogen use in photosynthesis of *A. arenaria* compared to *Elymus mollis*, but also a higher partitioning of carbon to its live leaves. This can explain the high biomass production that *A. arenaria* exhibits on Californian beaches.[61,62]

Specific phenology

Dormancy (+). *Ammophila arenaria* is a perennial plant with a long growth period, but with an innate dormancy of seeds.[53]

Unusual photosynthetic pathway (–). *Ammophila arenaria* is a C_3 plant like most of its grassy companions on the European dunes.

Attributes related to demography

Sexual reproduction

Early reproductive maturity (–). It takes at least two and usually more years before inflorescences of *A. arenaria* develop.[53]

Non-specialized seed production patterns (+). From the tolerance that *A. arenaria* exhibits to various extreme habitat factors, one can assume it bears a fairly non-specialized seed production pattern. Healthy clumps of *A. arenaria* can produce more than 30 000 caryopses per year.[62] Further towards the backdune area the number of developed caryopses per floret decreases.[53]

High resource allocation to seed production (?). The impressive number of 30 000 seeds per clump of *A. arenaria* that were estimated in one instance[63] suggests a high resource allocation to seed production. However, no studies have been carried out to prove this.

Long dispersal of seed in space (–). Seed dispersal of *A. arenaria* in space has not yet been studied in detail. The seed is small and light and is easily carried away by the wind. However, it does not bear particular structures that could facilitate the spread by wind or animals further than a few hundred metres.

Long dispersal of seed in time (+). Seed dispersal in time is probably more important as *A. arenaria* seed germinates better after storage.[53] According to W.H. Van der Putten (Netherlands Institute of Ecology, Heteren, pers. comm.) seed can be stored at about 5 °C for a couple of years without losing viability.

Vegetative reproduction

Rhizomatous or stoloniferous reproduction (+). *Ammophila arenaria* exhibits vigorous vegetative growth. It develops an extensive system of both horizontal and vertical rhizomes, which develop tussocks of the grass over a large area. The tussocks act as sand traps and trigger the formation of high and broad dunes.[64,65] It is this system of strong rhizomes that makes *A. arenaria* such an excellent binder of sand.

Attributes related to genetics

Plasticity

Genetic variability (?). No studies have addressed the genetic variability of *A. arenaria*. In a comparison of adaptation in *A. arenaria* with the European dune grass *Puccinellia maritima*, the former exhibited high levels of phenotypic flexibility while *P. maritima* showed both phenotypic flexibility and genetic differentiation.[66]

Polyploidy (+). *Ammophila arenaria* is a tetraploid species with a normal chromosome number of $2n = 28$, but higher polyploidy levels can occur. A chromosome count of Polish *A. arenaria* found that $2n = 56$.[53] In Polish *A. arenaria*, polyploids may result during the development of antipodals.[67] However, it is important to note that around 70% of all angiosperms are polyploid anyway.[68]

Non-specialized pollination patterns (+). *Ammophila arenaria* is wind pollinated.

Specific mating system

Autogamy (?). There are records of protogyny in the Mediterranean variety *A. arenaria* var. *arundinacea*, leading to autogamy.[53] No such records exist for the northern and western European variety *A. arenaria* var. *genuina*, whose flowers appear to be strongly protandrous. As it is apparently the latter variety that was introduced to South Africa,[9] the South African strain of *A. arenaria* is unlikely to be capable of autogamy.

Apomixis: vegetative apomixis and/or agamospermy (–). *Ammophila arenaria*'s capability of vegetative apomixis has been described above. Agamospermy, on the other hand, is not evident in *A. arenaria*; the species is known to be amphimictic.[53]

Potential attributes of South African Cape coastal dunes favourable for invasion (Table 3)

Habitat attributes

Ecosystem subject to frequent natural or man-made disturbances (+)

Coastal and urbanized environments are the two most disturbed ecosystems on earth.[31] Coastal dunes suffer continual gross disturbances through natural causes such as wind and wave action.[69] This applies to any coastal system but in particular to extensive mobile dunefields, of which there are examples along the South African Cape coast. The South African coastal conditions are among the most extreme in the world with average wind speeds of more than 20 km h^{-1} in windy seasons, frequent gales and a high-energy ocean.[70]

Existence of open spaces (+)

The continuous disturbance of coastal dune ecosystems causes frequent breaks in the natural plant cover. Communities of recent origin and early successional stages, like foredune communities, are particularly prone to invasion.[52,71]

Existence of spare resources (–)

Soils of sand dunes are characterized by a low nutrient status and low water-holding capacity. Extreme habitat conditions plus the usual stresses of competition, predation and diseases make the dune environment one of the most hazardous to inhabit.[72] This applies strongly to the South African dunes.[70]

Ecosystem homoclimatic to home territory (–)

Only the southwestern part of the South African Cape coast has a Mediterranean-type climate similar to some of *A. arenaria*'s natural range in Europe.[53] The entire Cape coast is characterized by extremely strong winds. Furthermore, there are no regular frost periods along this coast as there are in Europe, including parts of the Mediterranean littoral, which could affect germination. Rainfall is lower in South Africa, radiation higher, and daily temperatures subject to stronger fluctuation.[73,74]

Evolutionary history with isolation patterns, e.g., islands, continental endings (+)

The South African coastline represents the southernmost edge of the African continent and exhibits 'insularity' conditions.[31]

Biotic attributes

Absence of predators (–) *and competitors* (?)

Ammophila arenaria in its natural range is exposed to predation by rabbits and insects.[53] Grazing by herbivores has not been observed on South African dunes, and a negative impact of insects needs further investigation, but is unlikely. The extent of competition that *A. arenaria* is exposed to on South Africa dunes is unknown and should be addressed.

Absence of pathogens (?)

The decline of *A. arenaria* in semi-fixed and fixed dune sands with increasing organic matter content may be due to the negative impact of biotic soil factors such as fungi and nematodes.[75–78] A reason for the uninhibited growth of *A. arenaria* along the west coast of North America, even in comparatively stable dunes further inland,[18] could be the lack of soil-borne pathogens. Preliminary studies indicate that *A. arenaria* declines in vigour in fixed dune sands in South Africa owing to the harmful influence of parasitic nematodes.[9] This needs further examination.

Possibility of new mutualistic relations (?)

Studies of the rhizosphere in European *A. arenaria* stands indicate that nitrogen-fixing root bacteria such as *Bacillus* spp. and *Azotobacter* play a vital role in *A. arenaria*'s nitrogen nutrition.[79–81] It is also suggested that vigorous growth of *A. arenaria* is related to the development of vesicular-arbuscular mycorrhizae.[75] No nitrogen-fixing bacteria were detected in stands of Californian *A. arenaria*,[22] although an abundance of endomycorrhizal fungi was found in their roots.[18]

Table 3. Attributes that make a site susceptible to invasion (adapted and modified from ref. 26). (+) applies to South African Cape coastal dunes, (–) does not apply to these dunes, (?) not known whether applicable to South African Cape coastal dunes (see text).

Habitat attributes:	ecosystem subject to frequent natural or man-made disturbances (+)
	existence of open spaces (+)
	existence of spare resources (–)
	evolutionary history with isolation patterns, e.g. islands, continental margins (+)
Biotic attributes:	absence of predators (–) and competitors (+)
	absence of pathogens (?)
	possibility of new mutualistic relations (?)

Rating of *A. arenaria* as a potential invader compared with other South African invasive plant species

The use of lists of species and habitat attributes known to facilitate biological invasions provides valuable information in the case of *A. arenaria* in South Africa: as indicated in Tables 2 and 3, a large number of warning signs of a potential invasion were found to be positive both for *A. arenaria* and the South African Cape coast. The grass is characterized by a remarkable ecological tolerance and vigorous rhizomatous reproduction. It bears many physiological and demographic traits which enhance invasiveness. The Cape coast is a highly dynamic system dominated by early-successional species. Furthermore, it has an evolutionary history with isolation patterns. Both features may enhance its invasibility and we have scored it at about 14 for total invasive characteristics. Since *A. arenaria* has invasive characteristics and could become a problem plant, it is rated at only 1 for invasive potential (Table 4).

When one compares the invasive characteristics and the appropriate habitats of other known invasives in South Africa, a further picture of the potential invasiveness of *A. arenaria* emerges (Table 4). Although we do not have detailed information on all the other species (Table 1), we have characterized some invasives to compare with marram grass. *Acacia cyclops* and *Chronolaena odorata* are woody shrubs that have invaded temperate and subtropical biomes, respectively. They have high site invasive potential and also a majority of plant species' invasive characteristics and therefore many invasive characteristics (>20) and the highest invasive impact of 10 (Table 4). Weedy ruderals which are fairly widespread, such as *Bidens bipinnata* and *Tagetes minuta*, while not having as high an invasive impact (<6), are also well endowed with invasive characteristics (>20). These species are mainly abundant in disturbed agricultural lands, so their impact is not as high as the woody shrubs which invade many habitats. Even species such as *Opuntia ficus-indica* and *Sesbania pancea*, which are under moderate biological control and with medium invasive impact (6 and 4, respectively), have a number of invasive characteristics (>16). Thus the number of invasive characteristics of *A. arenaria* (~14) certainly places it in the class of the other invasive plant species in South Africa.

Further studies required on *A. arenaria*

So far, the examination of warning signs of invasiveness and invasibility in the case of *A. arenaria* and the Cape coast is based on theoretical assumptions. It is now desirable to implement observational and experimental investigations on the biology of *A. arenaria* in South Africa. Research in a wide range of areas such as the community biology, demography, reproductive behaviour and population genetics of marram grass as well as its interactions with soil pathogens in South African dune systems will give a more powerful indication on whether it is invading — or likely to invade — coastal dune systems. It will also shed new light on the *A. arenaria* problem of the North American Pacific coast[13,15,16] and contribute to a better understanding of the grass and its biology in different environments.

The assessment of the invasive potential and influence of non-indigenous plant species has recently been examined by Parker *et al.*[82] They point out that the rating of invasion impacts has been carried out only in general terms, and suggest using a quantitative measure. Their index is based on the range of the species, its average abundance and effect of the individuals as biomass. This method of comparing species is in its infancy but should prove useful. Researchers in South Africa should follow this approach as a further method to assess potential invaders such as *A. arenaria*.

Conclusions

This study shows that, despite the restricted predictability of biological invasions, the assessment of a risk for invasion can in well-determined cases be usefully achieved through lists of attributes. South Africa is the only place, apart from Europe, where the grass is still extensively planted.[9] Although plantings are still carried out in Australia (G. Druett, Department of Land and Water Conservation, Nowra, Australia, pers. comm.), a stabilization site like the Tableview/Blouberg Strand (Fig. 1 B) site near Cape Town, with kilometres of *A. arenaria* plantings, is surely unique, and possibly a short-sighted undertaking. Although our knowledge of *A. arenaria* and various biotic features

Table 4. Invasive characteristics of *Ammophila arenaria* and site invasive characteristics compared with some other invasive plant species in South Africa.

Species	Invasive species characteristics (maximum of 21 — Table 2)	Site invasive characteristics (maximum of 9 — Table 3)	Total of invasive characteristics (maximum of 30)	Invasive potential or severity of impact (see Table 1)
Ammophila arenaria	11	3	~14	1
Woody shrubs — extreme invaders				
Acacia cyclops	~14	~8	~22	10
Chromolaena odorata	~17	~8	~25	10
Weeds of cultivation				
Bidens bipinnata	~15	~6	~21	2
Tagetes minuta	~14	~6	~20	6
Weeds under some biological control				
Opuntia ficus-indica	~13	~5	~18	6
Sesbania punicea	~11	~5	~16	4

of the Cape coast is not sufficient to allow further predictions, the present study confirms that concern about the further planting of *A. arenaria* in South Africa is not unreasonable

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