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Plant traits and spread of the invasive salt marsh grass, *Spartina alterniflora* Loisel., in the Great Brak Estuary, South Africa

JB Adams[1]*, A Grobler[1], C Rowe[1], T Riddin[1], TG Bornman[2] and DR Ayres[3]

[1] *Department of Botany, Nelson Mandela Metropolitan University, PO Box 7700, Port Elizabeth 6031, South Africa*
[2] *South African Environmental Observation Network, Elwandle Node, 18 Somerset Street, Grahamstown 6140, South Africa*
[3] *Evolution and Ecology, 2320 Storer Hall, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA*
* *Corresponding author, e-mail: janine.adams@nmmu.ac.za*

Spartina alterniflora **Loisel., widely recognised as an aggressive invader of estuaries and salt marshes around the world, was discovered growing in the temporarily open/closed Great Brak Estuary on the southern Cape coast of South Africa in 2004. This is the first record of this invasive plant in Africa as well as its first occurrence in an estuary that closes to the sea. Plant traits and sediment characteristics were measured in 2009 and 2011 and found to be comparable to those reported elsewhere. Prior to the 2011 sampling,** ***S. alterniflora*** **stands had been flooded for almost eight months. As a result, sediment redox potential (−268 + 4 mV) was significantly lower in 2011. Sediments were mostly clay in 2009 (71 ± 0.01%) compared to a predominance of sand in 2011 (40 ± 0.02%). These differences were related to the artificial breaching of the estuary one month prior to sampling in March 2011. The grass currently occupies 1.1 ha in the salt marsh, sandflat and mudflat habitats of the estuary where its cover is expanding at a rate of 0.162 ha y^{-1}. Individual stands numbered about 12 in 2006, but have increased to 24 in 2011. These stands are expanding laterally at 0.9 m y^{-1} although the long period of inundation during 2010 reduced this to 0.6 m y^{-1}. Expansion is due to vegetative spread as an analysis of the sediment seed bank showed no** ***S. alterniflora*** **seeds and very few salt marsh seeds (1 132 seeds m^{-2}). If left unchecked,** ***S. alterniflora*** **has the potential to replace 42.9 ha or 41% of the total estuary habitat in the Great Brak Estuary, but also has the potential to invade other estuaries in South Africa, especially those with extensive intertidal habitat and containing** ***S. maritima*** **(19 estuaries in total). This study illustrates the adaptive potential of this invasive marsh plant and indicates the possibility of invasion in seasonally closed estuaries in other locations around the world.**

Keywords: biomass, closed estuary, cordgrass, expansion rate, habitat loss, intertidal habitat

Introduction

Spartina alterniflora is native to the Atlantic and Gulf coasts of North America, occurring as far south as northern Argentina. It is a major invasive grass along the USA Pacific coast, in China and New Zealand (Ayres et al. 1999, Chung 2006). The ecological impact that this species has had on the estuarine environment now overshadows the engineering benefits (e.g. An et al. 2007). It invades open intertidal mudflats, converting them into dense monospecific marshes and results in direct habitat loss (Hedge et al. 2003, Wang et al. 2006). *Spartina alterniflora* invasions also cause a trophic shift from an algal- to a detritus-based foodweb, owing to belowground biomass of *S. alterniflora* being five times larger than aboveground biomass (Simenstad and Thom 1995, Levin et al. 2006). As a result, richness and diversity of fish, and shore and wading birds are reduced (Callaway and Josselyn 1992, Daehler and Strong 1996, Neira et al. 2006, Wang et al. 2008). In Willapa Bay, Washington, USA, the introduction and spread of *S. alterniflora* resulted in a 20% reduction in habitat for aquatic birds. Besides habitat loss, there have also been numerous reports on changes in benthic community abundance and composition (Levin et al. 2006, Neira et al. 2006) and altered trophic function (Chen et al. 2009).

In South Africa, *Spartina maritima* (Curtis) Fernald occurs in 19 of the larger estuaries that are permanently open to the sea (Adams et al. 1999). It forms an important habitat for invertebrates such as the salt marsh crab *Sesarma catenata*. Worldwide, this species occupies a wide and discontinuous range from Western Europe to North, East and southern Africa. Pierce (1982) reported that *S. maritima* may have been introduced into South Africa based on Marchant and Goodman's (1969) proposal that this species had a tropical origin since plants growing in warmer regions were more vigorous than those from temperate regions. However, the origin of this species in South Africa is still unknown (Yannic et al. 2004). *Spartina maritima* has been replaced extensively in Britain by *Spartina anglica* (Mobberley 1956, Marchant 1967, Marchant and Goodman 1969, Ayres and Strong 2001). Both *S. alterniflora* and *S. anglica* are capable of spreading rapidly due their fertile seeds (Zedler and Kercher 2004), unlike *S. maritima* which rarely sets seed (Marchant and Goodman 1969). Of the 19 estuaries in South Africa in which *S. maritima* occurs, intertidal salt marsh area totals 1 264.22 ha (van Niekerk and Turpie 2012), which could be potentially lost through hybridisation with *S. alterniflora* (Strong and Ayres 2009) and expansion into existing intertidal salt marsh.

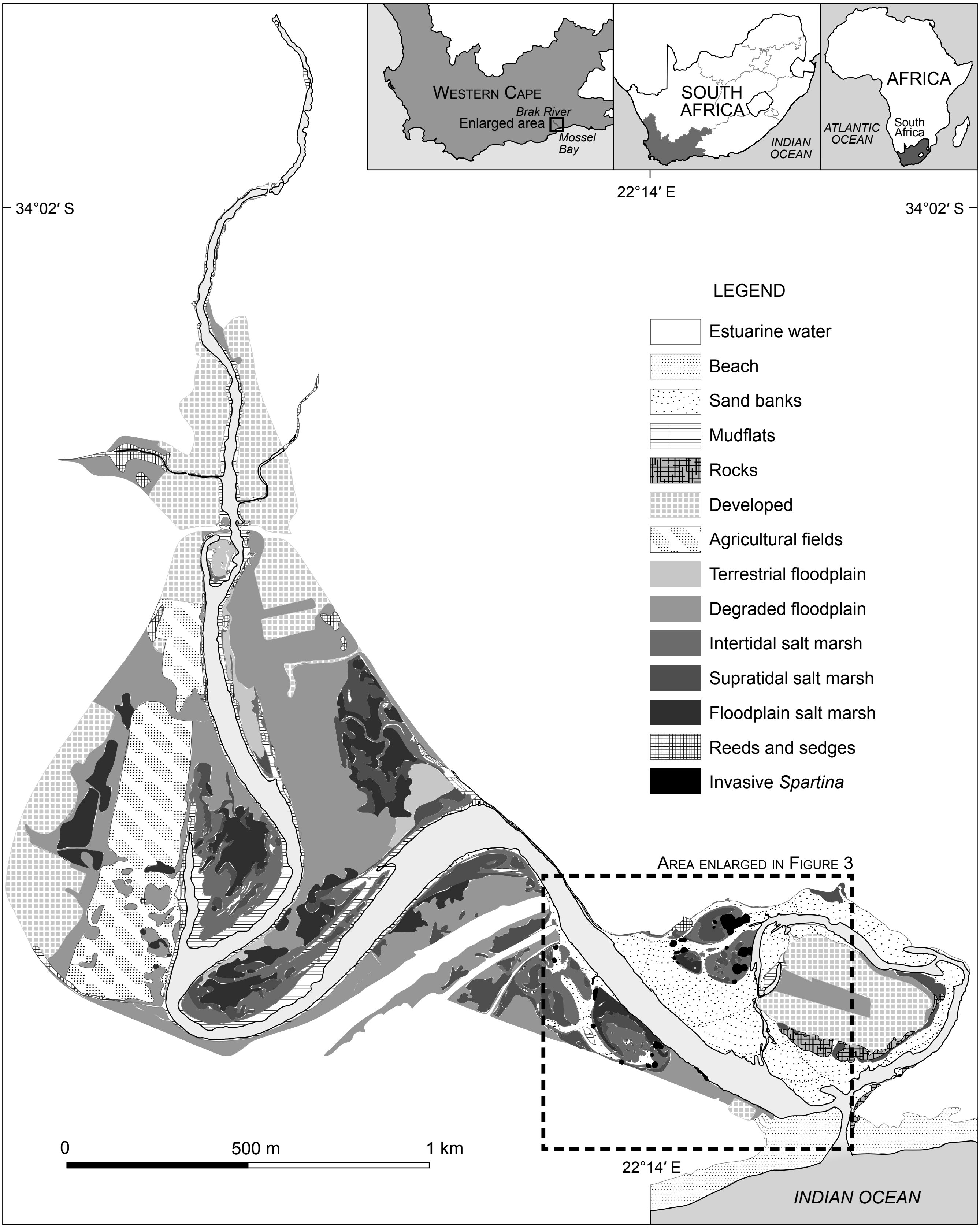

Figure 1: Location of the Great Brak Estuary on the southern coast of South Africa and the distribution of different habitats and land uses in the estuary The expansion of *Spartina alterniflora* stands in the lower reaches of the Great Brak Estuary from 2006 to 2011 is shown in Figure 3

Cordgrass plants with morphology consistent with *S. alterniflora* were observed for the first time in a South African estuary, the Great Brak, in 2004. This was the first time *S. alterniflora* was recorded in a system that closes to the sea and where the stands are inundated for months at a time. The Great Brak Estuary is classified as a temporarily open/closed estuary (Whitfield 1992). The mouth closes off to the sea through the development of a sand berm and remains closed for extended periods. Most (71%) of South Africa's estuaries are periodically closed at the mouth. *Spartina maritima* is not present in these estuaries as it only occurs in permanently open estuaries in South Africa (Adams and Bate 1995).

This study reports on the spread of *S. alterniflora* in the Great Brak Estuary and compares the plant and sediment characteristics with published records. It also assessed the seed bank of *S. alterniflora* stands and adjacent intertidal salt marsh. Based on experiences elsewhere, the potential impacts of this invasive grass on the estuary are outlined and recommendations are made on how to control the population and prevent further spread.

Material and methods

Study site

The Great Brak Estuary is located 24 km to the east of Mossel Bay on the southern Cape coast of South Africa (34°03′23″ S, 22°14′25″ E) (Figure 1). This estuary falls within the warm temperate coastal region (Whitfield 1992) has an average rainfall of 520 mm y^{-1} and average daily temperatures of 7–19 °C in winter and 15–26 °C in summer (Morant 1983). The estuary is relatively shallow (0.5–<2 m deep) with deeper areas (3–4 m) occurring between 2 and 4 km from the mouth (Morant 1983). The construction of the Wolwedans Dam, 3 km upstream of the head of tidal influence of the estuary, was completed in 1989. This has reduced freshwater input to the estuary and increased closed mouth conditions. The subsequent implementation of a mouth management plan, together with water releases from the dam, have mitigated some of the potential impacts. The management plan ensures that the mouth remains open during spring and summer, because these are important times for the growth and germination of salt marsh plants, as well as fish and invertebrate recruitment from the sea into the estuary (Adams et al. 1999, Huizinga 2003). During this study, artificial breaching of the mouth took place on 4 July 2009 and 1 February 2011 (Figure 2). Under closed conditions, water level in the estuary may increase through rainfall or marine overwash events to 2–3 m above mean sea level (msl) depending on the height of the berm. At the time of sampling in both 2009 and 2011, the mouth of the estuary was closed (Figure 2). Prior to sampling in 2009 the *S. alterniflora* stands were flooded for about three months. By comparison, in 2011 more than 50% of the *S. alterniflora* stands would have been inundated for around eight months (Figure 2). This is because *S. alterniflora* occurs at an elevation range of 0.63–1.29 m above msl. Under flooded/inundated conditions, soils were waterlogged and approximately 50% of the aerial parts of the grass were inundated.

Salt marshes in the Great Brak Estuary show distinct zones, influenced by tidal inundation when the mouth is open. Between 1.25 and 1.5 m above msl, the salt marsh consists of a mixed zone of *Sarcocornia decumbens* (Tölken) A.J.Scott, *Limonium scabrum* (Thunb.) Kuntze and *Bassia diffusa* (Thunb.) Kuntze and is characteristic of the upper intertidal salt marsh. Between 0.89 and 1.22 m above msl, *Sarcocornia tegetaria* S.Steffen, Mucina & G.Kadereit, *Cotula coronopifolia* L., *Triglochin bulbosa* L. and *Triglochin striata* Ruiz & Pav. are dominant. *Sarcocornia pillansii* (Moss) A.J.Scott is the dominant supratidal salt marsh species in the middle reaches of the estuary. *Spartina maritima* (Curtis) Fernald is absent. The salt marsh and exposed sand and mudflat habitats in the lower reaches of the Great Brak Estuary are currently the sites of invasion for *S. alterniflora* (Figures 1, 3).

Genetic analyses

DNA from leaf samples of the suspect *Spartina* sp., along with leaves from the local *S. maritima* (collected from the

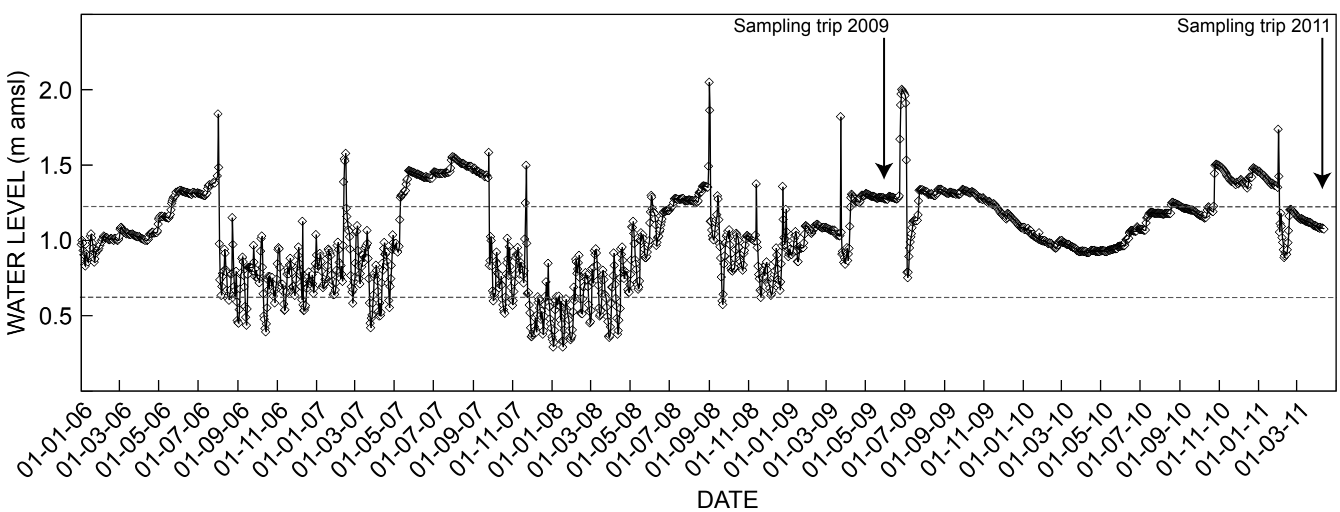

Figure 2: Water level in the Great Brak Estuary for the period January 2006–March 2011. Horizontal lines represent elevation of *Spartina alterniflora* stands

Kowie Estuary at 33°36′11″ S, 26°54′10″ E, were extracted (Daehler et al. 1999). Polymerase chain reaction conditions were as reported in Daehler et al. (1999) using the randomly amplified polymorphic DNA (RAPD) technique. RAPD primers that amplified DNA bands specific to either *S. maritima* or *S. alterniflora* (see Ayres and Strong 2001) were used. Electrophoresis was carried out according to Daehler et al. (1999) and scoring according to Ayres and Strong (2001).

Plant traits

Plant traits, such as height, stem density, aboveground and belowground biomass were measured in eight stands. For height, five quadrats (0.38 m × 0.38 m) were sampled within each stand, with quadrats transecting each stand. Quadrat A was on the water's edge, quadrat C in the middle and quadrat E on the landward edge of the stand. Belowground biomass, including roots and rhizomes, was subsampled within each quadrat from three 5 cm cores collected to a depth of 10 cm. Samples for biomass were oven dried at 60 °C until constant weight. Data were extrapolated to 1 m². Sampling for all traits was done from 24 to 26 April 2009. Plant height measurements for the eight stands were repeated on 26 March 2011 to determine the effect of prolonged inundation on the stands.

Physico-chemical characteristics

Sediment characteristics were measured to compare

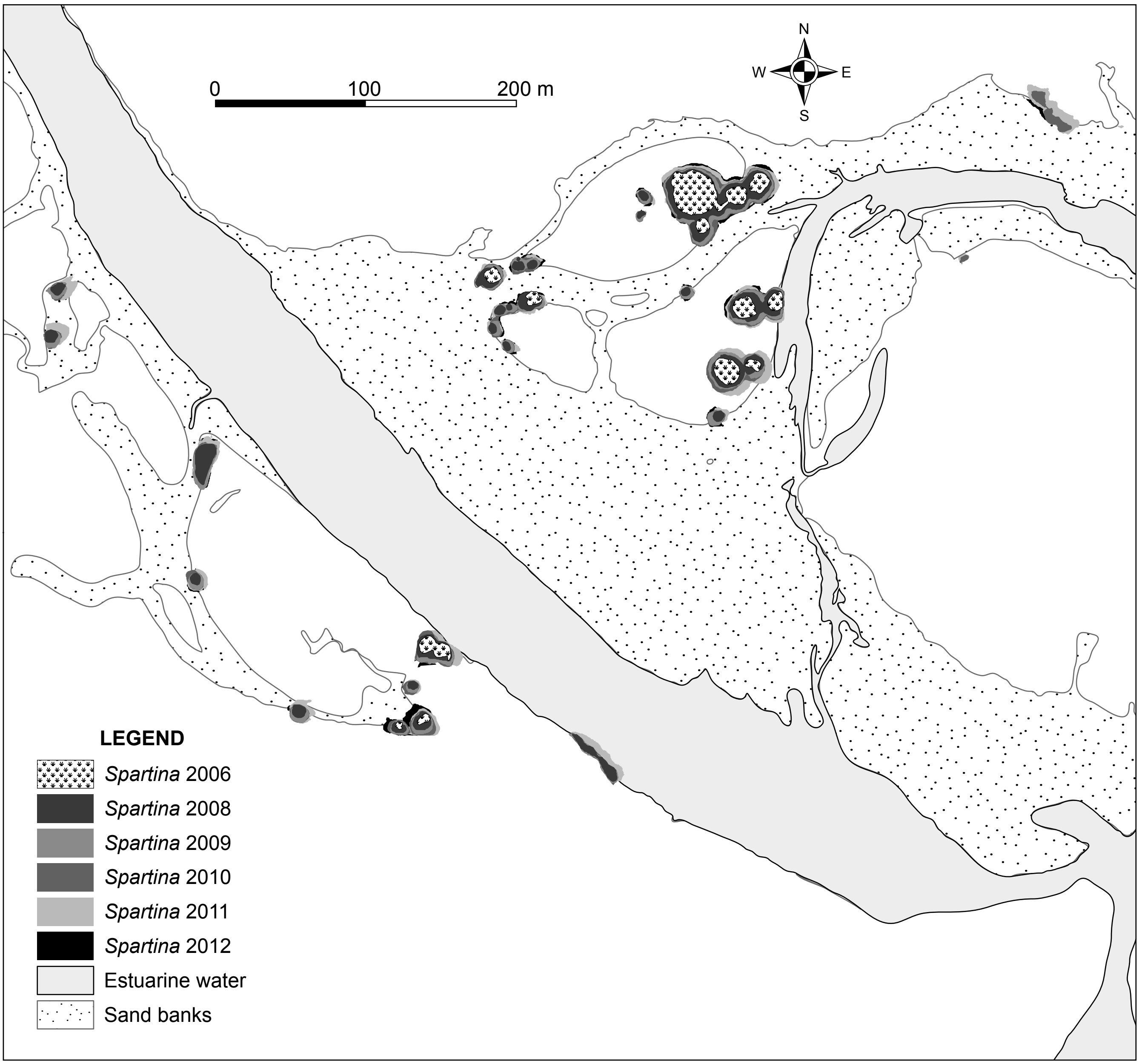

Figure 3: The expansion of *Spartina alterniflora* stands in the lower reaches of the Great Brak Estuary from 2006 to 2012

conditions with published records and to assess whether there were any changes over time. Sediment samples were taken in the same quadrats from the eight stands used for plant traits in April 2009 and March 2011. Samples were taken from the surface of the sediment to a depth of 5 cm. In March 2011, sediment samples were also taken adjacent to each of the eight stands; one in the open, unvegetated water channel where possible *S. alterniflora* expansion might occur (n = 8), as well as on the landward side in the existing salt marsh (n = 8). This was done to assess whether the invasion of *S. alterniflora* was changing sediment characteristics. All sediment samples were brought back to the laboratory for analysis of moisture content (%), organic matter content (%), electrical conductivity (mS cm^{-1}), redox potential (mV) and sediment particle size (%). Samples were analysed using the following methods: moisture content (Gardner 1965); organic content (Briggs 1977); electrical conductivity (Non-Affiliated Soil Analyses Working Committee 1990) using a Yellow Springs Instruments Company 30M/10 FT handheld conductivity meter; redox potential (Non-Affiliated Soil Analyses Working Committee 1990) using a Metrohm AG9101 electrode; and particle size using the hydrometer method (Gee and Bauder 1986). Water column temperature (°C) and salinity were sampled at six sites along the length of the estuary from the mouth to the head.

Seed bank collection and analysis

Five sites were sampled to assess sediment seed bank reserves for *S. alterniflora* habitat and to compare this with the salt marsh habitat. At each site, 20 sediment cores (6 cm diameter and 5 cm deep) were randomly collected within a 10 m × 10 m plot. To account for the spatial heterogeneity of seed distribution, samples for each site were aggregated into separate buckets (one for each site). The buckets were closed and stored at 4 °C until analysis. In the laboratory, a sodium hexametaphosphate $(NaPO_3)_6$ solution of 50 g l^{-1} was added to each bucket and mixed on a mechanical shaker for 10 minutes. The dispersal and deflocculating properties of the solution allowed the seeds to be separated from the sediment and other organic particles. The flotsam was then poured over paper towelling that absorbed the water and only the seeds and other organic matter remained. This was left to air dry for 3–4 days at room temperature. Seed counting and identification was done by analysing the seeds under a dissecting microscope. Seed numbers were recorded and expressed as seed density m^{-2} for the different sites. All the seeds were placed in Petri dishes in a growth cabinet at 24 °C for three months and allowed to germinate to test their viability. Regular checks for germination were made every three days.

Expansion rate

The distribution of *S. alterniflora* in the Great Brak Estuary was mapped in the field in October 2006, February 2008, April 2009 and March 2011 using a GPS and ArcPad® (Version 7.0) software. The data were analysed using ArcGIS™ 9.3.1 (ESRI®) to determine the change in total areal cover and lateral expansion rates of *S. alterniflora* stands.

Statistical analysis

Statistica, Version 10 (2011), was used for statistical analysis. A Shapiro-Wilks test was applied to test for normality. For data that were non-parametric, a Kruskal-Wallis ANOVA test was applied.

Results

Genetic analyses

The suspect *Spartina* sp. contained all DNA bands specific to *S. alterniflora* and no bands specific to *S. maritima*. Conversely, the *S. maritima* samples contained all bands specific to *S. maritima* and no bands specific to *S. alterniflora*. Thus, the suspect plant was considered to be *S. alterniflora*.

Plant traits

Plant height ranged from 0.66 to 1.4 m with a significant increase in plant height in 2011 compared to 2009 (p < 0.005, n = 48) (Table 1). However, plants on the water's edge in 2011 appeared shorter than those on the landward side of the stands. This, together with a considerable amount of dead material towards the centre of the stands, was related to eight months of prolonged inundation as a result of closed mouth conditions. Average stem density in 2009 was 217 stems m^{-2} and ranged from 55 to 429 stems m^{-2} (Table 1). The aboveground biomass of *S. alterniflora* ranged from 625 to 1 185 g m^{-2} and belowground biomass from 1 982 to 4 463 g m^{-2}. Belowground biomass was highest in the centre of the *S. alterniflora* stands, decreasing significantly toward the water's edge (p < 0.001). The root:shoot ratio of *S. alterniflora* ranged from 1.89 to 5.32 and was also significantly higher in the centre of each stand, decreasing towards the water's edge (p < 0.001).

Physico-chemical characteristics

Average water column salinity in 2009 was 22 (SD 0.6) and temperature 18.6 °C (SD 0.3) whereas in 2011 the average water column salinity was 19 (SD 0.1) and temperature 22 °C (SD 0.1). Historically, salinity usually drops to between 5 and

Table 1: Comparison of plant and sediment characteristics of *Spartina alterniflora* in the Great Brak Estuary for 2009 and 2011. Standard errors are given in parentheses

Characteristic	2009	2011
Plant characteristics		
Plant height* (m)	0.72 (0.04)	0.96 (0.15)
Stem density (m^2)	217 (34)	–
Aboveground biomass (g m^{-2})	933 (147)	–
Belowground biomass (g m^{-2})	3 120 (493)	–
Root:shoot ratio	3.6 (0.8)	–
Sediment characteristics		
Water content (%)	37.5 (0.02)	14 (0.01)
Organic matter (%)	2.96 (0.0)	2.47 (0.0)
Redox* (mV)	−228 (4.49)	−268 (3.98)
Sand* (%)	16 (0.02)	40 (0.02)
Silt (%)	15 (0.01)	13 (0.01)
Clay* (%)	71 (0.01)	48 (0.02)

* Significant difference (p < 0.001)

15 prior to breaching due to release of fresh water from the Wolwedans Dam. Sediment redox potential was significantly lower in stands in 2011 (−268 mV, SD 3.98) compared to 2009 (−228 mV, SD 4.49; $p < 0.001$, $n = 88$). *Spartina alterniflora* stands had significantly higher clay content than either silt or sand in 2009 ($p < 0.001$, $n = 88$). However, in 2011, sediments had significantly higher proportions of sand ($p < 0.005$). There were no significant differences for any of the other measured sediment characteristics between 2009 and 2011 (Table 1). Comparison of sediment in the *S. alterniflora* 2011 stands with the open water channel and the adjacent landward salt marsh showed that only sediment redox potential in the adjacent salt marsh was significantly higher (marsh = −90.9 mV, SD 84.1; *Spartina* stands = −268.4 mV, SD 35.6) ($p < 0.05$, $n = 8$).

Seed bank assessment

In 2011, *S. alterniflora* was flowering at the edges of the stands but no seeds were observed in the flowers and no seed was found in the sediment. In addition, no seedlings were observed and plants appeared to be expanding vegetatively. The average density of salt marsh seeds was low (1 132 seeds m^{-2}) with a few dominant genera (*Sarcocornia*, *Ruppia*, *Schoenoplectus* and *Salicornia*). Only 13% of the seeds germinated and were therefore viable.

Expansion rate

In 2006, *S. alterniflora* occupied a total area of 0.26 ha. This was made up of 12 distinctive circular stands with a mean size of 213.8 m^2 (SD 84.2) (Figure 3). In 2008, there were 27 stands and in 2009 and 2011 this had decreased to 23 and 24 stands respectively due to stands merging. Stand size increased over time from 327.7 m^2 (SD 112.9) in 2009 to 425.9 m^2 (SD 124.2) in 2011. Areal cover of *S. alterniflora* also increased, from 0.79 ha in 2009 to 1.1 ha by March 2011. This represents an overall increase of 207% from when it was first measured in 2006, representing an annual increase in cover of approximately 41.4%. Since 2006, the aerial cover of *S. alterniflora* expanded at an average rate of 0.162 ha y^{-1} (SD 0.002). Analysis of the change in *S. alterniflora* stand-radii between 2006, 2008, 2009 and 2011 showed that *S. alterniflora* clones expanded laterally at an average rate of 0.9 m y^{-1} (SD 0.1). Between 2009 and 2011, when there was a period of long inundation of about eight months, lateral expansion rate decreased to 0.6 m y^{-1}.

Discussion

This study reports the first record of *S. alterniflora* in Africa, as well as its first occurrence in a temporarily open/closed estuary. In estuaries worldwide, *S. alterniflora* occupies the lower- to mid-intertidal area with tidal inundation of up to 12 h per day (Callaway and Josselyn 1992). McKee and Patrick (1988) found that *S. alterniflora* expands with increasing tidal amplitude. However, in the Great Brak Estuary, the mouth remains closed for between three and eight months of the year, mainly during the winter. During this closed period, *S. alterniflora* stands become inundated for up to eight months, but we found that this did not seem to have an adverse effect on growth as plant traits were similar to those reported elsewhere. Lateral expansion rate did, however, decrease due to this prolonged inundation. It also resulted in highly reduced sediments (sediment redox potential −195 to 354 mV) within the *S. alterniflora* stands. Sediment redox potential was also significantly lower in 2011 than in 2009. One of the main characteristics that sets this species apart from other *Spartina* species is its ability to tolerate anaerobic flooded conditions, made possible by large amounts of aerenchymatous tissues (Teal and Kanwisher 1966) and the ability to oxygenate its roots and rhizosphere (Howes et al. 1981, Naidoo et al. 1992).

Plant and sediment traits measured in this study are comparable to those reported in the literature (Tables 2, 3). Average aboveground (933 g m^{-2}) and belowground biomass (3 119.7 g m^{-2}) of *S. alterniflora* in the Great Brak Estuary were in the lower range reported for other sites. Although *S. alterniflora* in our study was shorter (average height 0.72 m) than that reported for invasive populations elsewhere, biomass was higher (Table 2). This was a result of the high stem density of up to 429 stems m^{-2}, which was higher than that reported for most other invasive populations (Table 2).

An average root:shoot ratio of 3.6:1 was recorded in this study, which was in the lower range of that reported in other studies (4:1–11:1 generally, and as high as 49:1, Gallagher 1974). The observed trend of linearly increasing plant height toward the water-side of stands in 2009 and the fact that plants were significantly taller at the water-side than at the centre of clumps in 2009 suggests that the height of *S. alterniflora* increase in response to short periods of inundation (about three months prior to 2009 sampling). *Spartina alterniflora* invests more of its resources in increasing its height where inundation is highest so as to prevent the plant from becoming entirely submerged. However, long periods of inundation with brackish waters (salinity <19) appears to reduce plant height, as in 2011 the plants on the water's edge of the stands were significantly shorter than on the landward side. Mendelssohn and Seneca (1980) showed that under stagnant, standing-water conditions, growth of *S. alterniflora* was inhibited. Linthurst and Seneca (1981) also showed that increased salinity and flooding (Linthurst 1979) decreased aboveground and belowground biomass, stem density and plant height. Extended inundation and submergence can lead to root oxygen deficiencies, elevated soil sulphide concentrations and decreased plant N uptake which eventually reduces plant productivity (Wilsey et al. 1992). In South Africa, *S. maritima* only occurs in permanently open estuaries. The absence of this plant from temporarily open/closed estuaries was related to the plant's requirement for tidal flooding and saturated substrata associated with intertidal habitats that are generally absent from these types of estuaries (Adams and Bate 1995). However, the regular artificial opening of the Great Brak Estuary creates intertidal conditions and exposes bare sandflats and mudflats thus facilitating colonisation by *S. alterniflora*. It is unknown how the plant arrived at the Great Brak Estuary.

No seeds of *S. alterniflora* were found in the sediment, but the recruitment of 12 new stands suggests vegetative spread in the Great Brak Estuary. Salt marsh species were also poorly represented in the sediment seed bank. The salt marsh is therefore expected to establish through vegetative spread when *S. alterniflora* is removed. In March 2011, *S. alterniflora* was flowering but no seeds were found

Table 2: Characteristics of *Spartina alterniflora* reported in available literature and comparison with data from the present study

Location	Plant height (m)	Density (individuals m^{-2})	Biomass aboveground ($g\ m^{-2}$)	Biomass belowground ($g\ m^{-2}$)	Source
Invasive sites					
Great Brak Estuary, South Africa	0.66–0.87	55–429	615–1 185	1 982–4 463	This study
San Francisco Bay, California, USA	ND	ND	1 800–2 000	1 775–2 222	Callaway and Josselyn (1992)
Willapa Bay, Washington, USA	~1.6–1.8	~281–320	~600–1 500	ND	Grevstad et al. (2003)
Yangtze Estuary, China	Up to 2.5	ND	1 600–2 600	5 000–7 200	Li et al. (2009)
Chongming Dongtan, Shanghai, China	~1.5	~215	ND	~1 600	Wang et al. (2006)
Wangang Estuary, China	0.46–1.61	61–109	71–605	83–455	Zhou et al. (2009)
Native sites					
Sapelo Island, Georgia, USA	1.08–1.53	100–209	1 915–2 174	ND	Christian et al. (1983)
Great Marsh, Delaware, USA	0.37–1.21	314–1 139	266–1 349	754–1 044	Gross et al. (1991)
Parangua Bay, Brazil	0.5–1.0	200–750	125–800	400–950	Netto and Lana (1997)
Altamaha River, Georgia, USA	ND	80–140	900–1 900	3 000–6 000	Schubauer and Hopkinson (1984)
Hog Island, Virginia, USA	0.28–0.56	380–561	270.4–976.9	ND	Tyler and Zieman (1999)

ND = no data available

Table 3: Sediment characteristics associated with invasive and native *Spartina* stands and comparison of data from this study in the Great Brak Estuary, South Africa

Species	Organic matter (%)	Redox potential (mV)	Water content (%)	Sand content (%)	Silt content (%)	Clay content (%)	Location	Source
Invasive sites								
Spartina alterniflora	0.5–7.1	–437 to –52	2–61	0–87	0–41	7–96	Great Brak Estuary, South Africa	This study
Spartina alterniflora × *foliosa*	3.7	−27	ND	~60	ND	48.6	San Francisco Bay, California, USA	Neira et al. (2006)
Spartina alterniflora	0.3–5.5	ND	ND	ND	ND	22–34.8	Willapa Bay, Washington, USA	Paveglio et al. (1996)
Native sites								
Spartina alterniflora	ND	ND	ND	55.5–91.6	3.6–32.1	4.8–12.4	Dean Creek, Georgia, USA	Christian et al. (1983)
Spartina alterniflora	0–25	ND	~30–80	ND	2–98	0–4	Parangua Bay, Brazil	Netto and Lana (1997)
Spartina alterniflora	0.7–4.5	−80 to 125		ND	2.3–60.1	9.5–26.8	Hog Island, Virginia, USA	Tyler and Zieman (1999)
Spartina alterniflora	2–2.2	ND	ND	ND	15.8–25.6	43.3–52	Hackensack Meadowlands District, New Jersey, USA	Yuhas et al. (2005)
Spartina foliosa	~4.5	ND	ND	~4.1	~25.3	~70.6	Tijuana Estuary, USA	Ward et al. (2003)

ND = no data available

in the inflorescences. The absence of seeds is encouraging given that floating seeds were responsible for virtually the entire invasion of Willapa Bay (Civille et al. 2005) and San Francisco Bay (Ayres et al. 2004, 2008). Rhizome fragments made virtually no contribution to the spread of *S. alterniflora* and hybrid cordgrass in these estuaries. As observed in Willapa Bay, Washington, the established stands will continue to spread laterally until they coalesce into large meadows unless stopped by some type of plant management (Civille et al. 2005).

Spartina alterniflora has spread by 207% in the Great Brak Estuary since 2006 at an annual rate of increase of 0.16 ha y^{-1} (SD 0.002) (approx. 41% annual increase in cover). This rapid increase in cover is greater than the 12% annual areal growth rate of *S. alterniflora* recorded for Willapa Bay. Lateral expansion rates of 0.9 ± 0.1 m y^{-1} were measured in the Great Brak Estuary but decreased to 0.6 m y^{-1} due to the long period of inundation. This is within the range reported in published literature. Radial growth of 0.5 m y^{-1} (Sayce 1988), 0.793 m y^{-1} (Feist and Simenstad 2000) and up to 2.7 m y^{-1} (Xiao et al. 2010) have been recorded.

Expansion of *S. alterniflora* in the Great Brak Estuary is currently taking place in habitats with an elevation of 0.63–1.29 m above msl and displacing intertidal salt marsh species such as *S. tegetaria*, *Triglochin* spp., *C. coronopifolia* and *B. diffusa*, as well as the intertidal seagrass *Zostera capensis* Setchell. These plants occur in the Great Brak Estuary in the lower to upper intertidal marsh area. Intertidal salt marsh currently represents 13 ha of the Great Brak Estuary and benthic intertidal sandflats and mudflats 29.9 ha.

If left uncontrolled, *S. alterniflora* has the potential to replace 42.9 ha of habitat, or 41% of the total estuarine vegetation. Another concern is that the grass may spread to and invade estuaries adjacent to the Great Brak Estuary. *Spartina maritima* is rarely known to flower and set seed (Marchant and Goodman 1969), which limits its ability to colonise or maintain itself and makes it particularly vulnerable to extirpation should *S. alterniflora* invade estuaries where *S. maritima* is present.

High accretion rates of up to 26 cm y^{-1} have been reported under *S. alterniflora* canopies elsewhere (Chung 2006). Sediment accretion will likely raise the elevation profiles of existing salt marsh in the Great Brak Estuary, resulting in further habitat loss. Open sandflats and mudflats in the Great Brak Estuary, the habitat of burrowing sand and mud prawns (*Callianassa kraussi* and *Upogebia africana*) and the bivalve *Loripes clausus*, and their associated foodwebs (Morant 1983), will likely be lost. Many of these invertebrates are harvested and used as bait in recreational fishing, as well as being important food sources for birds.

It is clear from numerous studies throughout the world that *S. alterniflora* rapidly invades sensitive salt marsh habitats with ecosystem-altering effects. This new record of *S. alterniflora* spread in a seasonally closed South African estuary illustrates the adaptive potential of this invasive marsh plant. In only three years, the invaded area in the Great Brak Estuary has almost tripled, despite the fact that the plants are inundated for months at a time. Seasonally closed estuaries are relatively common in areas with alternating wet and dry seasons, occurring along the Pacific coast of the Americas, in Africa, India and Australia (Ranasinghe and Pattiaratchi 2003). There are also a few seasonally closed systems along the USA's south and west coasts, particularly in California and Texas, and occasionally as far north as Long Island, New York (Gobler et al. 2005). Seasonally closed estuaries, previously regarded as unlikely habitat for *S. alterniflora* (Daehler and Strong 1996), must now be considered vulnerable to invasion.

In April 2011, the Working for Water Programme of the South African Department of Environmental Affairs initiated some control measures. Two trials were used to eradicate *S. alterniflora*, a chemical treatment using Kilo Max (a herbicide containing glyphosate at 700 g kg^{-1}) and mechanical removal of the aboveground and belowground biomass. The latter is a slow process with the potential for the root system to break off and cause further spread, as well as the disturbance of sediment. Mechanical control has been shown to be effective only for patches <10 m diameter (Daehler and Strong 1996); however, successful eradications have occurred when the invaded area is <10 ha in size (Rejmanek and Pitcairn 2002). Unfortunately, two months after control methods began, severe floods opened the mouth of the Great Brak Estuary and large mounds of dried *S. alterniflora* biomass were washed out to sea. Adjacent estuaries must be monitored to determine if spread has taken place through floating fragments. A second chemical treatment took place in October 2011. However, recent observations (April 2012) have shown the regrowth of the stands at the edges. Follow-up eradication is urgently required, and can only be considered successful when there is no sign of the invasive plant for three consecutive years (Rejmanek and Pitcairn 2002).

Conclusion

This study has shown that *S. alterniflora* has invaded and outcompeted native salt marsh at the Great Brak Estuary. Sediment and plant conditions were similar to that of invaded sites worldwide. However, this is the first record of this grass in an estuary that closes to the sea, indicating that the plant has a wide environmental tolerance range. Follow-up chemical control treatments are needed to control the infested areas. If these are not treated, costs are expected to rise dramatically with an increase in invaded areas. The potential to invade nearby estuaries is a major threat to the biodiversity of South African estuaries.

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