Journal of Coastal Conservation (2019) 23:461–471
https://doi.org/10.1007/s11852-018-0675-0

Long-lived seed banks of *Ammophila arenaria* prolong dune restoration programs

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Received: 11 July 2018 / Revised: 17 October 2018 / Accepted: 9 December 2018 / Published online: 3 January 2019

Abstract

Marram grass (*Ammophila arenaria* L. Link (marram grass; *Poaceae*) has been identified as a major threat to the biodiversity of temperate dune systems outside its natural range. Coastal management and conservation agencies in a number of countries have invested in dune restoration programs involving the removal of invasive species, including marram grass. We investigate the age, viability and the depth distribution of buried seeds of this dune grass within two foredunes in southern New Zealand. The germinability of seeds of known age was determined at St Kilda Beach, Dunedin, New Zealand, to derive a minimum age for the seedbank. Seed was extracted by coring through a foredune to layers of sand of known age based on a time series of foredune-beach profiles. The potential of marram grass to develop large seedbanks in ideal conditions of vigorous plant growth and rapid foredune accretion, was investigated at Mason Bay. Buried seed was extracted using hand-corers to a maximum depth of 4.01 m and tested for germinability. A high proportion of excavated *A. arenaria* seeds were viable at both sites, including seeds recovered from 4 m depth at St Kilda, estimated to be at least 21 years old. We found no trend of declining viability with increasing depth at Mason Bay, suggesting seed may remain viable for longer than 21 years. Persistent, long-lived, seed banks of *A. arenaria* develop in foredunes. Restoration programs aiming to eradicate this species are likely to be prolonged (years to decades) as a result of regeneration from seeds that re-enter the shallow seed bank as dunes erode.

Keywords Seed banks · Foredune · Dune restoration · Marram grass

Introduction

Understanding the nature of persistent seed banks of invasive species is critical to the design of coastal dune restoration and conservation programs. Seed banks are causing significant frustration for conservation managers as persistent seeds drive regeneration over time-periods of many years to decades (Holm et al. 1977; Rejmanek and Richardson 1996; Marchante et al. 2011). In the present paper we examine the seed persistence of an invasive dune grass *Ammophila arenaria* L. Link (marram grass, European beach grass) in foredune seed banks in southern New Zealand. *A. arenaria* is a relatively large-seeded, perennial grass (*Poaceae*, *Agrostidinae*), known to produce large quantities of seeds (Salisbury 1942, 1952), which germinate readily (Huiskes 1979; Bencie 1990). However, establishment from seeds is reportedly rare due to low seedling survival in mobile and arid dune environments (Gemmell et al. 1953; Huiskes 1977; Huiskes 1979). Nonetheless, even occasional seedling establishment plays an important role in the colonisation and invasion of *A. arenaria*, because of the ability of this species to spread rapidly by vigorous vegetative growth (Buell et al. 1995; Wiedemann and Pickart 1996; Hilton et al. 2005). Moreover, observations of continued recruitment during a dune restoration program in southern New Zealand, 20 years after the parent population last flowered (Konlechner and Hilton 2010), suggest that the potential for this species to form a long-lived seed bank has been underestimated (see, for example, Knevel 2001).

A considerable body of knowledge links seed longevity and density in soil seed banks to seed morphology,

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germination behaviour and habitat characteristics. Plant species with substantial, long-lived soil seed banks are often small-seeded annuals, or perennials, with hard-coated seeds (Thompson and Grime 1979; Baskin and Baskin 1988; Venable and Brown 1988; Thompson et al. 1993; Bakker et al. 1996; Thompson et al. 1998; Thompson 2000). Such seed banks are typically found in habitats characterised by temporally unpredictable disturbance, and for many species seed banks are vital for population persistence (Weiss 1984; Bakker et al. 1996; Moore et al. 2006; Shen et al. 2006; Vosse et al. 2008; Ge et al. 2013).

Seed banks in coastal dune systems may form wherever sand accumulates around vegetation, but conditions are probably optimal in the foredune environment. Foredunes are shore-parallel dune ridges that form at the rear of sandy beaches by sand deposition within vegetation (Hesp 2002). They accrete (build vertically) and prograde (build seawards) as sand is transported by aeolian processes from the beach to the crest and rear slopes or plateau of the foredune; thus they form through the regular, incremental deposition of sand within vegetation. Sand-colonising species such as A. arenaria grow vigorously in these conditions, trapping sand and seeds as the foredune accretes. Ongoing accretion will inevitably bury seeds, potentially to depths equivalent to the height of the foredune. The resulting seed bank will persist until the seeds lose viability or until the foredune is disturbed. The seaward face of the foredune (the stoss face) is more likely to experience disturbance by wave-forced erosion or by aeolian erosion during episodic storms and strong onshore winds. The sand eroded from the stoss face and blown across the foredune may accelerate the burial of seeds, including seeds lying on the surface of the foredune crest or plateau (in the case of very large foredunes) or seeds released as the stoss face is eroded. These short-term changes are superimposed on annual to decadal trends of foredune accretion and progradation as the foredune evolves. The rate of foredune growth will depend on the rate of sand supply and the nature of the vegetation cover. *A. arenaria* foredunes tend to be very stable. Blowouts (an erosional hollow created by wind removal of sand from a localised part of the dune ridge) seldom develop in these foredunes, although the development of minor gullies in the stoss face of the foredune is typical. The plateau and rear surfaces of the foredune are relatively stable, except that they are subject to sand deposition (Hesp 1988; Petersen et al. 2011). This stability is usually only compromised during dune restoration operations by management agencies or exceptional natural events (e.g. hurricanes, tsunamis).

Seeds dropped after flowering may (i) fall on the foredune surface and germinate in the shallow soil; (ii) be swept into the sea by wind or waves during a disturbance event or offshore winds; or (iii) be consumed by predators. The remainder may be buried by sand, either in situ, or following secondary dispersal (Fig. 1). Seed deposition following secondary dispersal is more likely across the plateau and lee slopes of an exposed foredune subject to strong onshore winds. Buried seeds may be destroyed by predators or pathogens, or may remain viable and enter the seed bank – an accumulation of seed some depth below the surface (in excess of a few centimetres), where conditions (temperature and humidity) favour dormancy. In the context of coastal dunes, Maun (2009) distinguished between a shallow (‘effective’) seed bank and a deep (‘disabled’) seed bank, however this distinction may not be easily applied in the dynamic foredune environment. In most environments deeply buried seeds do not contribute to an effective seed bank (Baker 1989), but the geomorphic dynamism of foredunes, where the addition or erosion of sand to depths of metres may occur during events that last hours or days, may quickly return deeply buried seeds to depths suitable for germination.

We refer here to the ‘effective seed bank’ as seeds buried to a depth that does not prevent germination. Seeds in the ‘deep seed bank’ cannot germinate, but these seeds remain viable and might germinate if disturbance returns it to the effective seed bank. In the case of *A. arenaria* germination might occur when dune dynamics returns seeds to a depth of approximately 7 cm or less. Disturbance of the substrate - erosion of sand by wind and the development of a blowout, for example - might return deeply buried (metres deep) seeds to depths where germination is possible (centimetres). However, if these seeds were to remain buried below this level indefinitely, they would eventually deteriorate and be lost (Maun 2009). Recurrent accumulation of sand between disturbance events can result in the relatively rapid and deep burial of seed. Burial experiments have demonstrated the potential survival of buried seeds from a range of coastal species, for at least 2.5 years, but concluded burial depth is an important control on seed bank formation (Zhang and Maun 1994). However, the logistical difficulties in locating deeply buried seeds have seen little empirical data on naturally forming seed banks in foredune

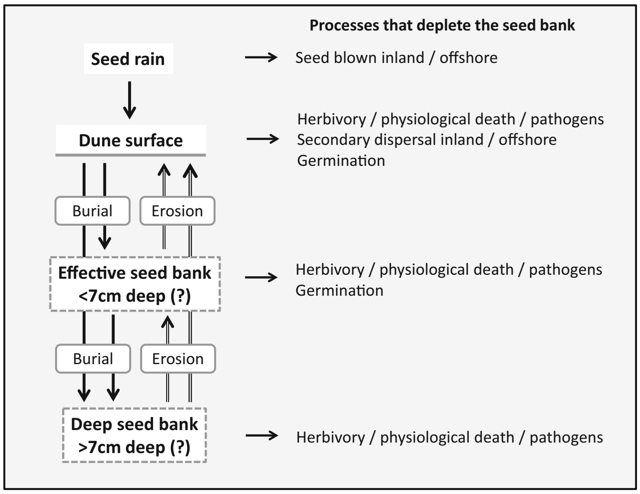

Fig. 1 *Ammophila* seed bank dynamics in foredunes (adapted from Maun 2009)

systems (Maun 2009). The current study addresses this issue by careful selection of field sites that afford a rare opportunity to determine the age of the deep seed bank of *A. arenaria*, and to quantify the magnitude of this seed bank in conditions of ideal plant growth, foredune accretion and seed-bank formation.

Seed burial and seed bank development in foredunes is likely to occur most effectively where the species of interest grow widely across the dune form (so that seed production is widespread and secondary dispersal by wind is impeded by the plant cover); the dune is stationary (albeit it may be subject to frequent minor and occasional major disturbance); and sand deposition occurs frequently. Situations where the establishment of an invasive plant has radically altered dune morphology, and the depositional environment, present an opportunity to investigate the formation and distribution of deep seed banks in a dune system, as seed bank properties can be linked to a known timeline of species introductions and landscape modification. A particular geomorphic form of foredunes formed in association with *A. arenaria* – Type I foredunes (described in Hesp 1988, 2002) - meet these conditions (Hilton 2006). This type of foredune is comprised of a continuous ridge of sand formed at the back of beaches with a steep seaward (stoss) face and semi-uniform and dense *A. arenaria* cover.

Observations of persistent regeneration of *A. arenaria* during a sustained eradication program led to the current study, which examines the extent and viability of the *A. arenaria* seed bank in two foredune systems in southern New Zealand. Both sites contain Type-1 foredunes that have formed in conjunction with *A. arenaria*. Both foredunes have a history of accretion, a process which should provide ideal conditions for seed burial. Most importantly, the age of layers of sand within one of the foredunes is known, allowing the age of seeds contained in those layers to be dated precisely. This affords an exceptional opportunity to determine the longevity of *A. arenaria* seeds, which is of the greatest significance to those with an interest in *A. arenaria* biology and dispersal; as well as those involved in managing *A. arenaria* outside its natural range. It was not our aim to compare the seed banks at the two sites – which have evolved in different conditions. Our approach is to utilise the unique characteristics of each site to address specific questions related to the seed ecology of *A. arenaria* - the presence and longevity of a deeply buried seed bank in the case of St Kilda Beach, and the size and spatial extent of the seed bank in the case of Mason Bay.

Materials and methods

Study sites

We sampled the seed bank of *A. arenaria* in two foredunes in southern New Zealand — St Kilda Beach (45°54' S, 170°31' E) and Mason Bay (46°55' S, 167°45' E) (Fig. 2). The Mason Bay foredune is located on the margins of a transgressive dune system situated on the west coast of Stewart Island – a high energy windward coast. This foredune formed following *A. arenaria* invasion by marine-dispersed rhizome in the late 1950s (Hilton et al. 2005). Progradation and accretion of the foredune following *A. arenaria* invasion has culminated in a relatively massive and stable foredune up to 11 m high and 120 m wide (Konlechner et al. 2016). The St Kilda foredune is, by comparison, a narrow landform, confined between a sandy beach and a dyke (locally referred to as 'John Wilson Drive') on the Dunedin metropolitan coastline. It formed after *A. arenaria* was planted on the back beach in 1980 to protect John Wilson Drive from storm-forced erosion. Prior to 1980 the site was a narrow beach, completely covered at spring high tides. Subsequent accretion has resulted in a stable foredune measuring up to 6 m high and 25 m wide which, like most stable *A. arenaria* foredunes in southern New Zealand, has a uniform morphology alongshore and which is not affected by blowouts.

The climate at both sites is cool-temperate, with average air temperatures ranging between 10 °C in winter and 16.5 °C in summer. Annual rainfall is 800 mm at St Kilda and 1600 mm at Mason Bay, and is evenly distributed through the year at both locations. In these conditions *A. arenaria* grows close to its climatic optimum (Konlechner et al. 2016). It flowers profusely on the stoss face of the foredune at both sites, although flowering has been less extensive at St Kilda since 2007 when the stoss face of the foredune was scarped during a storm event.

The history of progradation and accretion at both sites has been recorded by aerial photographs and topographic surveys. At St Kilda these surveys commenced in 1989, when the foredune was already 1.5 m high and 15 m wide. Regular surveys by registered surveyors and academics, between 1989 and 2009, recorded the continued vertical growth of the landward slopes of the St Kilda foredune, at an annual average rate of 0.25 $m.yr.^{-1}$ (Fig. 3). Further accretion ceased following scarping during storms and the height of the foredune has not changed since 2009. The 2014 profile is typical of the morphology of the foredune since 2009. The Mason Bay foredune prograded 75 m between 1958 and 1989 (Konlechner et al. 2016) – that is, the vegetation line shifted 75 m seawards during this period. Aerial photographs indicate that there was virtually no change in the position of the shoreline, as marked by the edge of the foredune vegetation, between 1989 and 1998. Between 1999 and 2014, during a period of annual foredune surveys, the foredune continued to accrete, but not prograde (Fig. 4), presumably because an equilibrium shoreline position was attained in 1989. Storm events occasionally scarp the foredune, however, in contrast to the foredune at St Kilda this erosion is relatively minor and has only affected the lower stoss face. There has been no blowout development since 1989.

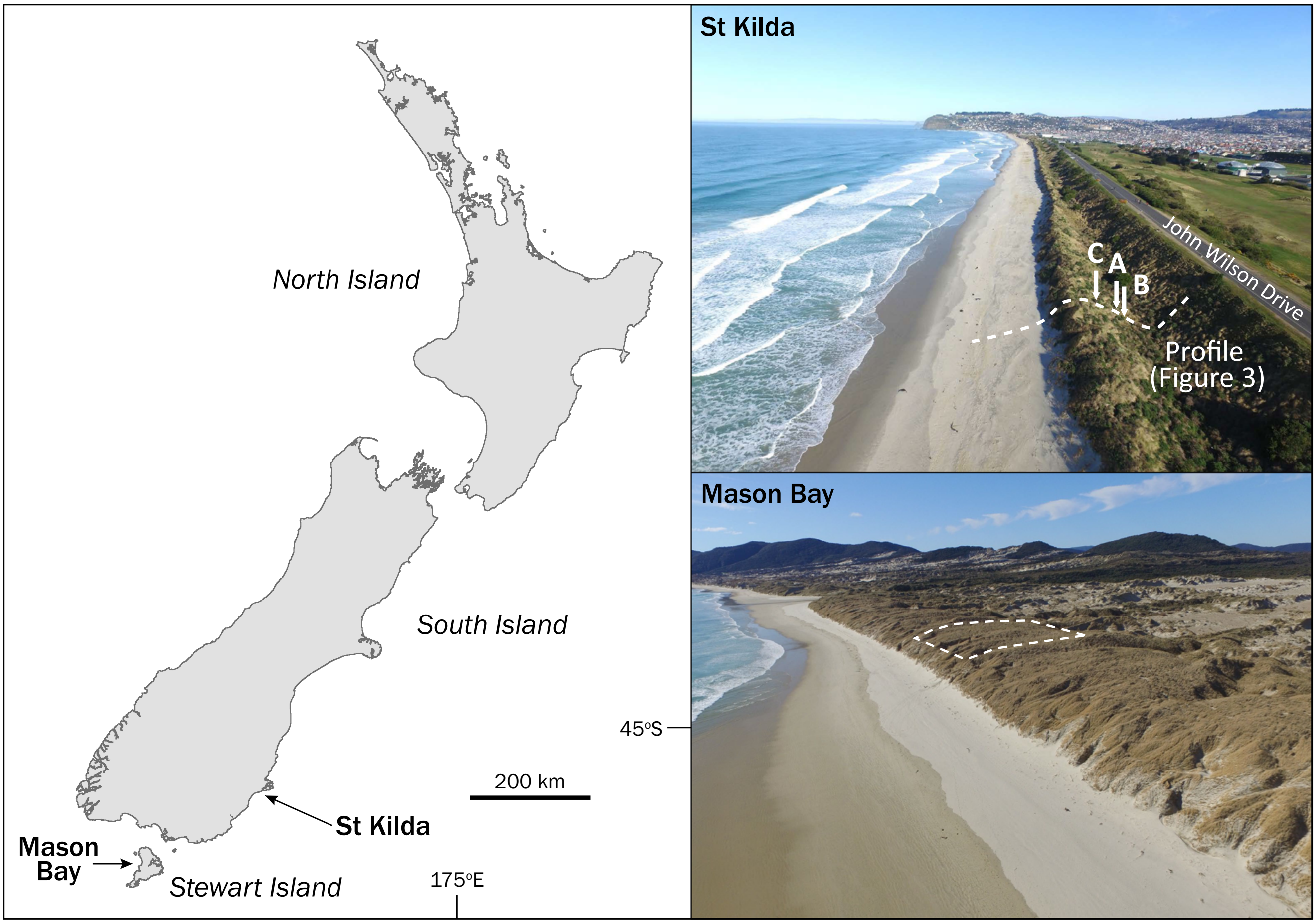

Fig. 2 *A. arenaria* seeds were extracted from a confined foredune on the south Dunedin coastline at St Kilda and from a large foredune at Mason Bay, Stewart Island (Rakiura). Both are stable foredunes that have accreted in conjunction with marram grass. The location of the cores reported (**a**-**c**) are indicated by the white arrows (St Kilda). The white rectangle indicates the area of the foredune upper stoss face and plateau cored at Mason Bay

These sites provide an exceptional opportunity to examine the seed bank of *A. arenaria*. Dune profiles document the systematic accretion of the foredune at St Kilda and the age of internal layers of sand, so it is an ideal site to investigate the presence and viability of a deeply buried seed bank. The foredune accreted between 1989 and 2009, so that the sand (and seed) can be effectively aged if the depth from which seeds are extracted is known. At any given depth the age of recovered seeds will accord with the age of the associated sand strata. The Mason Bay foredune is a relatively massive foredune that has developed in ideal geomorphic conditions in conjunction with a thriving *A. arenaria* cover. At this site

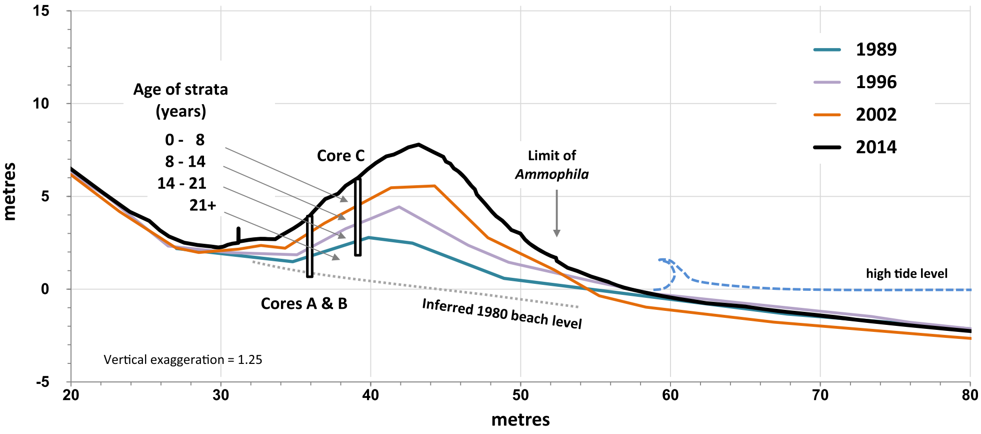

Fig. 3 The location of cores **a**, **b** and **c** across the St Kilda foredune, showing the surveyed profile lines and the inferred age of the intervening strata. The stoss face of the foredune was scarped in 2009 to the 46 m (from datum) mark

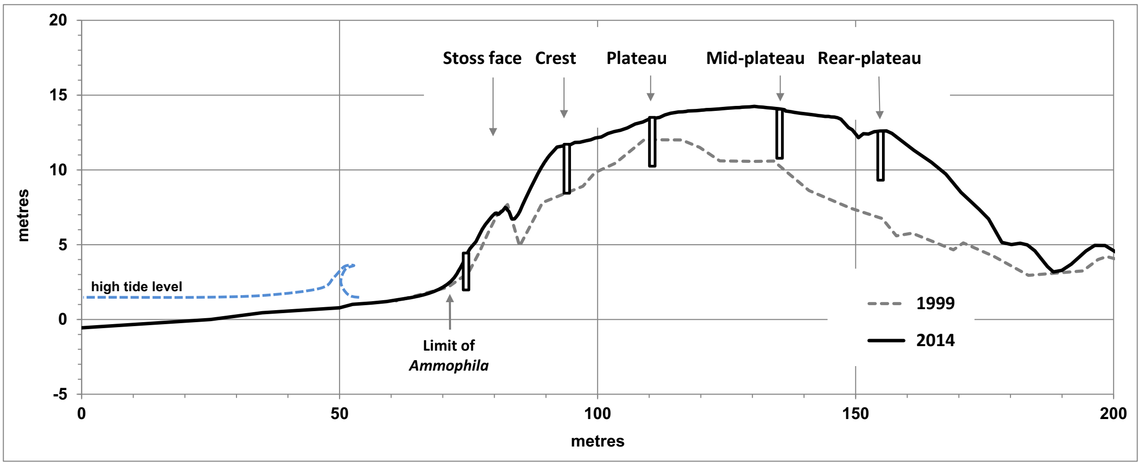

Fig. 4 The location of cores across transect 2 at Mason Bay. In addition, three cores were extracted across transects 1 and 3 adjacent to the stoss face, crest and first plateau cores. The foredune accreted 2-5 m between 1999 and 2014

our objective was to quantify the three-dimensional distribution of buried seeds and examine the spatial connect between seed production (flowering) and storage.

Seed Bank sampling

St Kilda

Samples were collected using an auger with a 0.20 m diameter in August and September 2010 (early spring). Three cores (A, B and C) were extracted from the rear slope of the foredune adjacent to the surveyed profile line (Fig. 3). Cores A and B were two metres north and south of the profile line, and core C two metres to the north of the profile line. As the objective was to obtain robust estimates of seed age for vertical sections of the seed bank we opted not to sample the crest and stoss face of the foredune to avoid the section of the foredune that might have been disturbed by scarping in 2009.

Each core was collected in contiguous increments (henceforth 'sub-samples') to a maximum depth of 4.01 m. Care was taken to core to a precise depth as the measured depth was used to infer the age of the recovered seed. The depth of each section of each core was carefully measured with a steel tape relative to a temporary peg surveyed to the benchmark used for the topographic surveys. Core A commenced 0.49 m below the surface because a section of the rear slope of the foredune had to be levelled to establish a working platform. Care was taken to prevent contamination of the core-hole sides and samples with surface seed.

The recovered seeds were split into four age categories based on the age of the associated strata, inferred from the foredune profile record. For example, seeds extracted below the depth of the 1989 profile, which occurred 2.5 m below the modern surface at the time of sampling in Core A and B, and 3.3 m below the surface in Core C, is inferred to be at least 21 years old at the time of extraction (Fig. 3). The differences in age classification were required because the different spatial positions of each core resulted in slight changes to the seed bank age-depth association. These categories and their corresponding depths are summarised in Table 1.

The depth and number of *A. arenaria* seeds in each sub-sample was determined using the extraction method, since it incorporates both germinable and dormant seeds (Meissner and Facelli 1999). Each sub-sample of sand was air-dried for one week at 20 °C, and then passed through a 1 mm analytical sieve to separate the seeds from the sand and other organic matter. All seeds were removed from their palea and lemma (where applicable) and subjected to a cold stratification treatment of 6.1 °C at 71% RH for 8 weeks (similar to the method used to test the viability of *A. arenaria* seeds in the Netherlands by Van der Putten (1990)). Seeds were then germinated in a Contherm Phytotron Climate Simulator, programmed with a fluctuating temperature regime and 14 h photoperiod (22 °C and 15 °C; 14 and 10 h) to simulate late spring/early summer conditions, consistent with the methods of Hendry and Grime (1993). Seeds were moistened with distilled water as required. After 45 days the number of germinating seeds per sub-sample was counted. The germination of seeds was recorded when the radicle became visible (after Van der Putten 1990).

Mason Bay

The seed bank at Mason Bay was sampled in April 2013 (autumn), after seed dispersal during February, and before germination was likely, using the same modified auger used at St Kilda. Assessing the number of seeds stored in the large foredune complex at Mason Bay posed a challenge. A strategy involving a large number of small samples would have been preferred, to compensate for the inevitable variation in subsurface seed distribution (see Brock et al. 1994), but such a strategy would have been impracticable. Instead 11 cores were

Table 1 A summary of the age groups of recovered seeds for each core at St Kilda and their corresponding sampling depths

Age categories (years)	Age of dune strata	Sampling depth (m) Core A and B	Sampling depth (m) Core C
0–8	2002–2009	0–1.0	0–1.4
8–14	1996–2002	1.0–1.9	1.4–2.4
14–21	1989–1996	1.9–2.5	2.4–3.3
21+	< 1989	2.5–4.3	3.3–4.2

extracted (in increments) along three shore-normal transects spaced approximately 20 m apart, within an area of 0.6 ha (Fig. 5). Cores were obtained from the stoss face, stoss peak and plateau (front, mid and rear) on Transect 2 (Fig. 4); but due to time limitations the mid- and rear-plateau, were not cored on Transects 1 and 3 (Figs. 4 and 5). At Mason Bay *A. arenaria* flowers across the foredune plateau, however, almost all flowering is restricted to the stoss face of the foredune with few inflorescences recorded across the stoss crest and plateau. The potential seed rain was assessed prior to coring by counting the number of inflorescences (formed during the preceding summer months) within a 1 m × 1 m quadrat centred on each core.

Each core was collected in 20 cm contiguous depth increments to a depth of 1.0 m (0–0.2, 0.2–0.4, 0.4–0.6, 0.6–0.8, 0.8–1.0 m), then every 0.4 m (1.4–1.6, 2.0–2.2 m, 2.6–2.8, 3.2–3.4 m) to a maximum depth of 2.2 m on the stoss face (the surface of the underlying beach facies, marked by a distinct lens of coarse sand), and 3.4 m in all other foredune environments. As at St Kilda the recovered seeds were split into age categories based on the age of the associated strata, inferred from the foredune profile record (Table 2). Cores were excavated to or below the 1999 surface (except for the rear plateau). Each sub-sample was sieved to separate the seeds from the sand and other organic matter and seeds were tested for germinability as described above.

Results

The presence and longevity of the *A. arenaria* seed bank at St Kilda

Seeds were recovered from the St Kilda foredune cores in low numbers (Table 3). A similar number of seeds was recovered from Cores A and C, but considerably fewer seeds were recovered from Core B. Overall the viability of the recovered seeds was high – between 83 and 87% for Cores A and C, and 57% for Core B. Most seeds (74% of all recovered seed) were found in sand layers deposited over a period of 8 years preceding fieldwork, but germinable seeds were recovered from all depths (Table 4).

The seed bank at Mason Bay

Germinable seeds of *A. arenaria* were recovered from all the Mason Bay cores (Table 5). The number of seeds extracted from each core was spatially variable, but the low number of seeds recovered makes it difficult to compare seed density between dune zones. Seed viability per core ranged between 42% and 90% with no clear spatial pattern between the three transects or across the foredune (shore-normal). There is, however, an indication that seeds extracted from the mid to rear plateau cores are less viable. Viable seeds were recovered

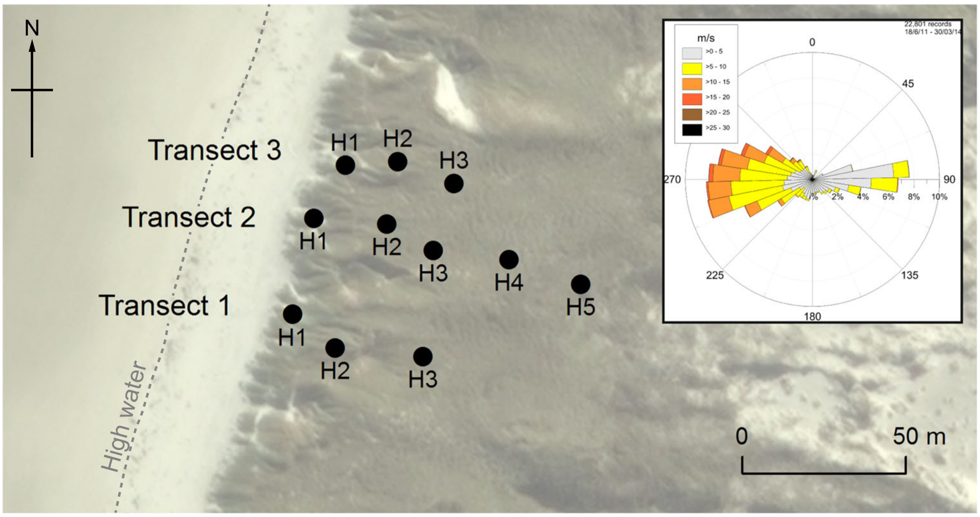

Fig. 5 Location of cores across the foredune in the Mason Bay study area. The wind rose, derived from observations over a 3-year period at a station near to 'H5', indicates the prevailing winds are primarily onshore

Table 2 The inferred age of seeds recovered from the Mason Bay cores based on the known rates of accretion

Age categories (years)	Age of dune strata	Sampling depth (m) stoss face	Sampling depth (m) crest	Sampling depth (m) plateau	Sampling depth (m) mid-plateau	Sampling depth (m) Rear- plateau
0–4	2009–2014	0–1.0	0–0.6	0–0.2	0–0.2	0–0.4
4–14	1999–2009	1.0–2.2	0.6–1.6	0.2–0.4	0.2–1.5	0.4–3.4
14+	<1999		1.6–3.4	0.4–3.4	1.5–3.4	

from the deepest core increments (2.2 or 3.4 m) at each core location. Cores extended below the surveyed 1999 foredune surface except at the stoss face and rear plateau core locations (along Transect 2), so that most of the seeds recovered from near the base of the cores are at least 14 years old. No trend in viability with depth was evident, suggesting the seed bank might extend well below the lower limit of coring. Approximately 8 m of foredune (aeolian) sand facies extends below the lowest core sample at the highest section of the foredune.

No strong trend in seed distribution with depth was evident, although in general seeds were more uniformly distributed in the plateau cores (Table 5). There was no correlation between the number of *A. arenaria* inflorescence counted in the quadrats and the total number of seeds recovered per core (Fig. 6a) or the number of seeds recovered from the upper 0.2 m of each core (Fig. 6b).

Discussion

Studies to date have typically ignored the role of seed banks in *A. arenaria* invasion. *A. arenaria* has successfully colonised many temperate dune-systems globally, usually to the detriment of the indigenous flora and dune ecology. It spreads from beach to beach by marine-dispersed rhizomes when foredunes are eroded by storm waves and rhizome is washed into the sea. It is then dispersed by nearshore currents, and may be stranded on a local or distant beach by waves, above the usual level of high tides (Konlechner and Hilton 2009). The spread of *A. arenaria* through hinterland dune systems, landward of the foredune, may then occur if seeds are blown inland; either from seeds released from flowering plants or from the seed bank when the foredune is disturbed. Prior to the present study it was not known whether *A. arenaria* formed persistent seed banks or whether seed banks should be considered in the invasion process or in strategies to eradicate *A. arenaria*. Here we have demonstrated that *A. arenaria* is able to form sparse, but persistent seedbanks in the foredunes of southern New Zealand.

Table 3 The number and viability of seeds recovered from Cores A, B and C (all depths), St Kilda foredune

	Core A	Core B	Core C
Number of seeds per litre of sand	0.32	0.05	0.24
Percentage seed viability	86.8	57.1	83.9

Seed persistence and viability

The recovery of germinable seeds from 3 to 4 m depth, estimated to be at least 21 years old at St Kilda and 14 years at Mason Bay, is a significant finding. This longevity is consistent with our observations of the ongoing emergence of *A. arenaria* seedlings at Doughboy Bay, 8 km to the south of Mason Bay, after the removal of above-ground *A. arenaria* and erosion of the dune surface (Konlechner and Hilton 2009 and subsequent observations by the first and second authors), and provides one of the longest estimates of seed bank longevity for plants in non-stable dune environments. Most investigations into seed banks in young dunal environments have focussed on quantifying seed density, with few estimates of seed persistence beyond 2.5 years (e.g. Zhang and Maun 1994). The biogeomorphic approach adopted in the present study has established that *A. arenaria* is able to form a persistent seedbank. The results of this study indicate the magnitude and viability of the seed banks of *A. arenaria* in two temperate foredunes with very different geomorphic histories. The density and distribution of seeds within other foredunes will depend on a range of biotic and abiotic factors unique to each foredune.

The incremental accretion of *A. arenaria* foredunes appears to promote deep seed bank formation. Calculated annual rates of sand accretion at St Kilda and Mason Bay would result, on

Table 4 Depth distribution of seeds and viability with depth in all St Kilda foredune cores

Age of seeds (years)	Number of seeds per litre	Percentage seed viability
0–8	0.61	84
8–14	0.09	88
14–21	0.05	100
21+	0.07	67

Table 5 The mean age distribution of seeds in all cores and the percentage seed viability with depth at Mason Bay

Number of seeds per litre of sand					
Inferred age of seeds (years)	Stoss face	Stoss peak	Plateau	Mid-plateau	Rear -plateau
0–4	0.57	1.47	0.37	0.16	0.48
4–14	0.03	1.64	2.02	0.57	0.80
14+		0.46	2.55	1.43	0.64
Percentage seed viability					
0–4	71	87	100	0	50
4–14	100	85	68	61	60
14+		92	60	76	50

average, in accretion (and seed burial) to depths of 0.13–0.20 m in the year following seed production. Emergence trials by the authors indicate that *A. arenaria* seeds are highly sensitive to light and unlikely to germinate and/or emerge from soil depths in excess of 0.07 m. Rapid burial, resulting in seeds being buried in conditions that inhibit germination, creates the necessary environment for the formation of a deep disabled seed bank. A younger, transient, seed bank may also form close to the surface, as has been found for other mobile dune species (Liu et al. 2007; Liu et al. 2011). With these

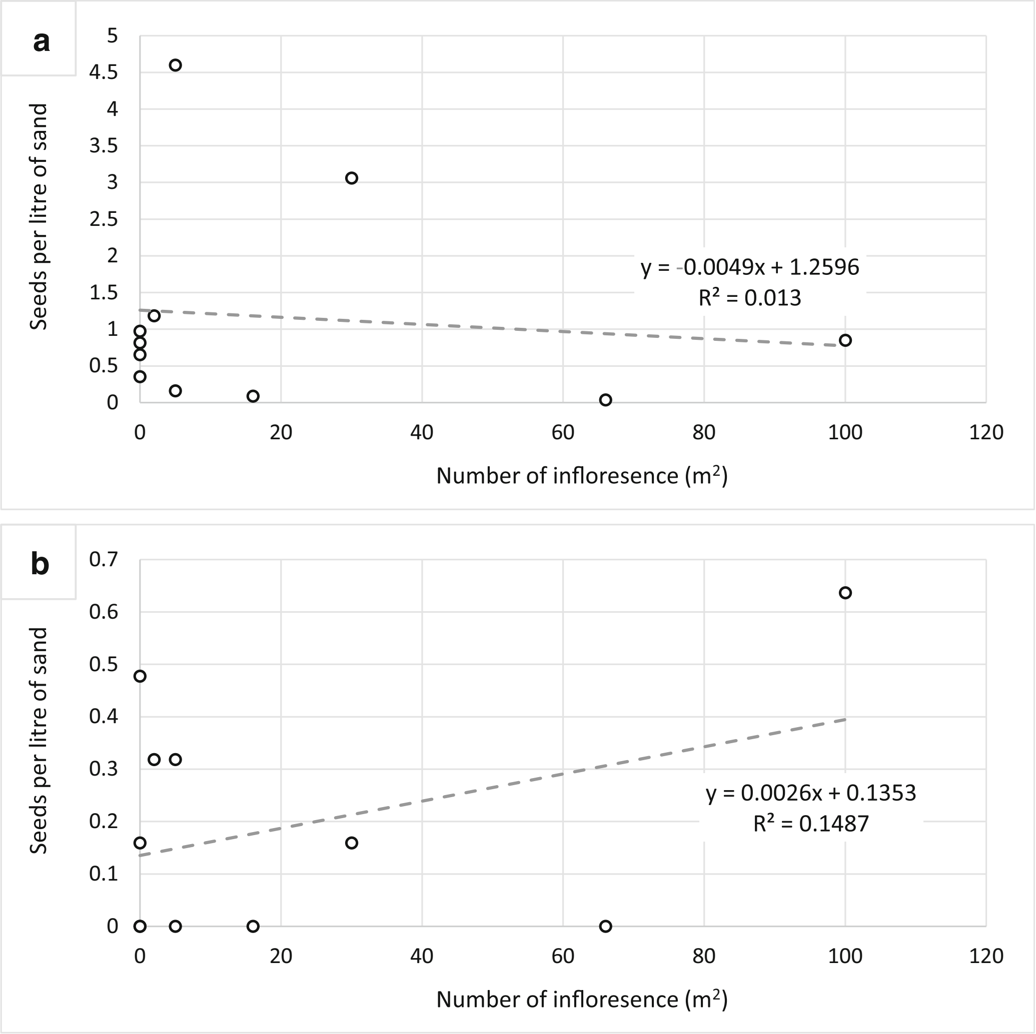

Fig. 6 **a** The total number of seeds recovered from each core vs. the number of inflorescence counted in the quadrat associated with each core location; **b** the total number of seeds recovered from the uppermost 0.20 m of each core vs. the number of inflorescence counted in the quadrat associated with each core

species, as with *A. arenaria*, a high proportion of seeds recovered from depth (0.4–1.0 m in these studies) proved germinable, suggesting this is a more widespread strategy among plant species on mobile dune systems. Our estimate of at least 21 years viability for *A. arenaria* seeds is probably not the maximum longevity of *A. arenaria* seeds, as no apparent trend of declining seed viability with depth was found at the St Kilda or Mason Bay sites. It is possible that *A. arenaria* seeds can remain viable for longer periods at similar and greater depths.

Seed bank density and vertical distribution

We faced significant methodological challenges excavating seeds at the two study sites. We found few seeds in the St Kilda foredune (though enough to indirectly age the viable seed). The Mason Bay foredune contained many more seeds, however, the height and width of the foredune, and the dependence on a manual coring technique, meant it was impossible to extract samples through the full depth of the foredune, and difficult to extract enough samples to characterise the three dimensional nature of the seed bank.

The Mason Bay coring suggest that *A. arenaria* has formed a widespread but low density seed bank in this large, stable, foredune. The low density of seeds recovered is somewhat surprising given the high seed output within the sampled areas at Mason Bay, but is consistent with the few estimates of seed density in dune systems elsewhere (e.g. Baptista and Shumway 1998). We note that there is a large population of rats (*Ratus* spp.) in the modern foredune so granivory may be significant.

We found that seeds were not uniformly distributed within the Mason Bay foredune. This was expected, based on observations of seed accumulation across the foredune surface during seed release. Following release seed is more likely to accumulate (and be buried) in depressions on the foredune surface. Seeds may accumulate in minor depressions (a few centimetres deep) on a ridge (metres high) on the foredune surface, but larger quantities of seeds will accumulate within gullies and larger depressions. Moreover, patterns of accumulation will likely vary through time as sections of the foredune experience fluctuating rates and patterns of sand deposition, and as the morphology of the foredune evolves.

Areas of greatest seed production and maximum seed storage were geographically separated - seed rain is highest across the stoss face, whereas the greatest density of buried seed was found beneath the rear plateau. The paucity of the seed bank below the stoss face is probably explained by the transport of seeds by winds as wind flow accelerates across the stoss face. Most of the seeds produced in this environment are probably exported by these winds or blown onto the beach and destroyed. In contrast the plateau is well vegetated, does not experience erosion and is accreting. Any seeds deposited (by wind) on this surface, that did not germinate immediately, are more likely to be buried and enter the seed bank. This indication of increased seed bank density with decreasing disturbance is consistent with findings for the majority of sand dune systems studied (e.g. Baptista and Shumway 1998; Ma et al. 2005; Liu et al. 2007; Leicht-Young et al. 2009; Liu et al. 2011).

Implications for management

The results of this study are highly germane to efforts to conserve the ecology of mid-latitude temperate coastal dune systems worldwide. Native to Europe, *A. arenaria* is now found on coastal dunes in most temperate parts of the world (Wiedemann and Pickart 2004). It threatens the natural character of temperate latitude coastal dune systems outside its native range, due to physiological adaptations that allow it to successfully compete for space with indigenous sand colonising species (Hertling and Lubke 1999). In the case of New Zealand, it has largely displaced the indigenous dune vegetation south of 39°S, and is a significant threat to the natural values of the remaining dune systems of high conservation value (Hilton 2006). Programs that aim to remove *A. arenaria* from dune systems of high conservation value have been implemented in parts of New Zealand (Moore and Davis 2004; Hilton and Konlechner 2010). Similar programmes are ongoing in parts of North America, Canada and Australia (Wiedemann and Pickart 2004). The ability of *A. arenaria* to disperse and reproduce by rhizome is now well documented (Hilton and Konlechner 2011; Konlechner et al. 2016), however, efforts to eradicate this species from coastal dunes of high conservation value are clearly being frustrated by regeneration from seed.

The Department of Conservation in New Zealand, for example, is currently engaged in a program to eradicate *A. arenaria* from Rakiura National Park on Stewart Island, New Zealand's third largest land mass (Hilton and Konlechner 2010). This program, which employs selective grass-specific herbicides, commenced at Doughboy Bay in 1999. Necrosis of the *A. arenaria* canopy and regeneration from rhizome was achieved in 2002 after three aerial (helicopter) applications of herbicide (Hilton and Konlechner 2010). However, the transition from intensive annual operations to the anticipated surveillance phase of the program (probably involving annual checks for stranded *A. arenaria* rhizome) has been long delayed by the annual emergence of *A. arenaria* seedlings (Konlechner and Hilton 2010). At this site the dune surface did not begin to erode until 2003, four years after the first herbicide treatment. Erosion was delayed by the decaying mass of *A. arenaria* culms and annual re-growth from buds on surviving rhizome (2000–2003). The substrate was exposed to wind from 2003 and the dune surface eroded, although erosion generally ceased following the exhumation of (dead) vertical rhizome of *A. arenaria* (Hilton et al. 2009). Thereafter, layers of the foredune have eroded as dead rhizome has been periodically exposed and decayed or been eroded by the wind. In this way the seed bank of *A. arenaria* has been progressively, incrementally, exposed and some seeds have germinated with each layer of sand eroded. The last *A. arenaria* plant flowered in 2000. However, seedlings are still emerging - the first author observed seedlings in February 2014 and the Department of Conservation sprayed seedlings in February 2016. Hence, the dune restoration program at Doughboy Bay continues long after the population of mature A. arenaria was eradicated. Conservation managers involved in *A.arenaria* eradication programs in temperate coastal dune systems should anticipate regeneration from the seed bank, and should consider a pre-treatment survey of the seed bank to ascertain the nature of the deep seed bank.

Conclusions

A. arenaria is an invasive coastal dune grass with a well-developed mode of vegetative reproduction from rhizomes. It has not previously been thought to form a persistent seed bank, but few studies have attempted to locate seed. Our observations of seedling recruitment following the eradication of the *A. arenaria* canopy suggested that seed banks play an important role in the ecology of this species. Excavations of buried seeds at two locations in southern New Zealand have confirmed that *A. arenaria* seeds can persist in the soil seed bank for at least 21 years. The formation of foredune *A. arenaria* seed banks is largely explained by geomorphic processes; the accumulation of sand on foredunes within populations of *A. arenaria* provides a mechanism for seed burial. However, seeds are more likely to accumulate downwind of the stoss face on windward coasts, trapped within the *A. arenaria* plant cover during periods of strong onshore winds. This is also the area of maximum sand deposition and hence seeds in this zone are more likely to be buried and buried deeply before they can germinate. Deep sampling is thus necessary to fully understand seed bank dynamics in foredune systems invaded by *A. arenaria*. Dune restoration programs should consider the potential for regeneration for a significant period of time - at least 21 years - following the initial treatment and foredune disturbance and erosion. Our findings also reinforce other studies of invasive plant species in dune systems - that invasion and persistence can be facilitated by a seed bank (Shen et al. 2006; Mason et al. 2007), and restoration programmes must incorporate long-term deep seed bank dynamics into management plans.

Acknowledgments This research was supported by a University of Otago Research Grant and a grant from the Department of Conservation (Southland Conservancy). We are very grateful to the staff of the Department for logistical support for our research and technical support from staff in the Departments of Geography and Botany at the University of Otago. Mr Chris Garden provided cartographic services for which we are very grateful.

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