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The search for indigenous dune stabilizers: Germination requirements of selected South African species

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Abstract. The coastline of South Africa is characterized by extensive dune fields which are threatened by development, and thus the demand of stabilization of drift sand will increase. The non-invasive alien grass species *Ammophila arenaria* is at present the dominant sand stabilizer. Due to its foreign origin and invasiveness in North America its use was criticized and indigenous sand-binding species would be preferred. The germination requirements of the native *Arctotheca populifolia*, *Ipomoea pes-caprae*, *Myrica cordifolia* and *Scaevola plumieri* were investigated. The results showed that for all four species the total germination time and germination phase could be shortened and germination success (number of germinated seeds) improved. The different scarification and stratification treatments broke the dormancy of *I. pes-caprae*, *M. cordifolia* and *S. plumieri*, whereas the seeds of *A. populifolia* were not dormant. Seeds of *I. pes-caprae* and *M. cordifolia* had induced an innate dormancy, respectively, whereas the type of dormancy in seeds of *S. plumieri* dormancy processes remained unknown.

Keywords: *Ammophila arenaria*; Dormancy; Dune pioneer; Foredune; Seed scarification; Seed stratification.

Nomenclature: Arnold & De Wet (1993).

Introduction

The movement of sand is a natural and intrinsic component of the dynamic coastal system, and the shape of dunes is constantly changing by erosion or accretion of sand in response to variable climatic and other environmental factors experienced along the coast. It was only when man started to develop and exploit the coastline that these natural drift sands posed a threat, and the need arose to prevent sand movement (Avis 1989).

At present the alien grass *Ammophila arenaria* is the most important drift-sand stabilizer in South Africa, but its use has been criticized on the grounds of its foreign origin and the proven facts of invasiveness in other parts of the world (Heyligers 1985; Buell et al. 1995; Hertling & Lubke 1999). Therefore, the use of indigenous stabilizers should be preferred and promoted by, for instance, planting seedlings or by sowing seeds in-between established pioneer vegetation to stabilize dunes. To be able to utilize the seedlings of indigenous species in these processes, knowledge about the germination requirements of these species is needed.

Arctotheca populifolia (*Asteraceae*), *Ipomoea pes-caprae* ssp. *brasiliensis* (*Convolvulaceae*), *Myrica cordifolia* (*Myricaceae*) and *Scaevola plumieri* (*Goodeniaceae*) all occupy the foredune habitat and have an excellent sand-binding capacity (see Tinley 1985). These species are known to be well adapted to grow in the fast moving sand substrate (e.g. Ripley 2001), and all produce numerous but very different diaspores. Information on germination under controlled conditions and field situations, as well as information on the fate of the seedlings helps to determine which species are good candidates to replace *Ammophila arenaria* for sand stabilising projects. Germination requirements of seeds can have a strong effect on the natural distribution of plant species and are therefore of interest in the timing of dune rehabilitation and restoration (Clark et al. 1995).

Seedlings of *A. populifolia*, *I. pes-caprae* and *S. plumieri* are often observed in the field (Knevel 2001), but not much is known about the seed ecology, and of the germination requirements and fate of seedlings in particular. Studies of dune species have shown that there are wide ranges of response to factors that affect germination, including soil moisture, temperature, light, and salinity (Fenner 1985; Priestly 1986; Bewley & Black 1994; Baskin & Baskin 1998). In addition seeds of unpredictable environments often show dormancy, preventing seeds from germinating under unfavourable circumstances (Baskin & Baskin 1998). On the basis of the before-mentioned information the present study aims at firstly breaking dormancy under controlled conditions; secondly determining the germination requirements; and thirdly monitoring seedling emergence and survival under field conditions.

Material and Methods

Seed collection and drying

The species *Arctotheca populifolia*, *Ipomoea pes-caprae*, *Myrica cordifolia* and *Scaevola plumieri* all produce very different diaspores with different dispersal modes (Table 1 and Fig. 1). All diaspores were collected in March 1998 (late summer) from the standing vegetation and air-dry ('air-dry'). For *A. populifolia*, *I. pes-caprae M. cordifolia* the diaspores were dried at room temperature (18 - 20°C), whereas the drupes of *S. plumieri* were dried more rapidly at 25°C to prevent fungal infections. For *I. pes-caprae* and *S. plumieri* seeds from the previous season(s) ('old') were also collected. The old seeds were collected from the sand surface (seed bank) before the seed rain in December 1998 (early summer). These seeds were considered to be at least one year old and had much thinner seed coats compared to the fresh seeds, probably due to sand abrasion.

The 'air-dry' and 'old' diaspores were kept in paper bags at room temperature until used. From here onward all diaspores will be called seeds, even when not true seeds.

Germination experiments

Germination experiments were conducted after collection in 1998 and after two and/or three years of dry-storage. Before the experiment the seeds were disinfected with a 70% bleach solution (3.5% sodium hypochlorite) and germinated in a controlled environment cabinet ('conviron') and the greenhouse.

In the conviron five replicates of 50 seeds each (due to petri dish capacity 30 seeds for *S. plumieri*) were placed on filter paper saturated with distilled water in 9 cm plastic petri dishes for 7 weeks. The seeds from *S. plumieri* showed no germination after 7 weeks and were left in the conviron for another 7 weeks. The seeds were germinated under a 25°C/15°C day/night temperature-regime and a light-regime of 16 hr /8 hr light/dark (Hertling 1997). The position of the petri dishes was randomized every 2-3 days when checked for moisture status and germination; the germinated seeds were counted and removed when the radicle was clearly visible. Ungerminated seeds were tested for viability on termination of the experiment by either squeezing the seeds upon a hard surface or cutting the seeds in half to inspect the embryo. Soft seeds with brown embryos were considered dead, whereas the hard/firm seeds with white embryos were considered viable (Baskin & Baskin 1998; Bekker et al. 1998).

For the greenhouse experiment three replicates for *A. populifolia* (air-dry), *I. pes-caprae* (air-dry + old) and *M. cordifolia* (air-dry) of 50 seeds each were placed 1 cm deep in trays filled with moistened beach sand. For *S. plumieri* the 30 ungerminated seeds from the conviron experiment ($n = 3$) were used. Temperature in the greenhouse was controlled with a mean day/night temperature

Fig. 1. From left to right two diaspores of each species: *Sacevola plumieri* (fresh and old), *Ipomoea pes-caprae* (fresh air-dry and old), *Myrica cordifolia* (fresh air-dry and fresh air-dry without wax and fruit layer), and *Arctotheca populifolia* (with and without the soft seed coat).

Table 1. Life form, diaspore type, diaspore weight (100 seed weight), diaspore size and main dispersal mode of the diaspores of *Arctotheca populifolia*, *Ipomoea pes-caprae*, *Myrica cordifolia*, and *Scaevola plumieri*. For all species the bare diaspore was measured, without easy detachable seed coats (*A. populifolia*), fruity layers (*S. plumieri*) or wax layers (*M. cordifolia*) (after Thompson et al. 1993).

Species[1]	Life form[1]	Diaspore type[2]	Weight[2] (g)	Size[2] (cm)	Dispersal mode
Arctotheca populifolia (*Asteraceae*)	Herb	Soft sunflower-like seed – ± 23 seeds per flowerhead	0.6	0.4 by 0.5	Geocarpy 3,4
Ipomoea pes-caprae (*Convolvulvaceae*)	Herb	Hairy seed with tough seed coat – 4-5 seeds per capsule	18.4	1.0 by 1.5	Autocarpy and Hydrocarpy 3,5
Myrica cordifolia (*Myricaceae*)	Shrub	Round berry with thick wax layer – 1 berry per flower	10.1	0.5 diameter	Zoocarpy 4
Scaevola plumieri (*Goodeniaceae*)	Shrub	Round stone in drupe with thick fruity layer – single-seeded drupe	57.6	1.1 diameter	Autocarpy and Hydrocarpy 3,6

[1] Arnold & De Wet (1993), [2] Knevel (2001), [3] Knevel et al. (2002), [4] Tinley (1985), [5] Devall (1992), [6] Muir (1937).

of 29°C/16°C without extra light sources (day length 12-16 hr). Germination trays were covered with perforated plastic sheets to prevent evaporation and checked every 2-3 days for moisture status and germinated seeds (seedling emergence) were counted and tagged.

Seed scarification and stratification experiments

To be able to use seedlings in stabilization projects many seedlings will be needed in a short time. In an attempt to speed up germination, different scarification and stratification experiments were carried out. As it is known that seeds of *I. pes-caprae* and *S. plumieri* survive months of submergence in seawater during dispersal (Muir 1937; Tinley 1985) and the seeds of *M. cordifolia* are protected by a wax layer (Tinley 1985), a boiling water scarification (wet heat) was carried out with these species. For the seeds of *I. pes-caprae*, *M. cordifolia* and *S. plumieri* also sulphuric acid scarification experiments and mechanical techniques (apical cutting) were carried out. Besides scarification, seeds of all four species (thus including *A. populifolia*) had a cold stratification period. Due to the high temperatures in the top layer of dune sand in spring and summer, a heat stratification experiment was carried out with *I. pes-caprae* and *S. plumieri* seeds. One control was used because all experiments ran simultaneously.

Wet-heat scarification

Per species five replicates of 20 seeds each were submersed in distilled water and kept at boiling point for periods of 1, 5, 15, 30, 60 and 240 min (Baskin & Baskin 1998).

Acid scarification

Per species five replicates of 20 seeds each were soaked in 0.5 M sulphuric acid for periods of 5, 15, 30 min and 2, 8 and 24 hr (after Hardcastle 1978). After submersion the seeds were rinsed thoroughly with tap water to remove the acid.

Mechanical scarification

Per species five replicates of 20 seeds each were mechanically scarified by cutting part of the seed coat off and subsequently placed in petri dishes on moist filter paper (Baskin & Baskin 1998).

Cold stratification

Per species five replicates of 40 seeds (*S. plumieri* 25 seeds) were placed between moist filter papers in petri dishes and kept dark and cool (5°C) for a period of 6 weeks (Hendry & Grime 1993).

Heat stratification

Per species five replicates of 20 seeds were placed 2 cm deep in crucibles filled with dry sterilized dune sand. The crucibles were placed in an electric oven for 8 hr at 45°C and 16 hr at 20°C for a period of two weeks. The crucibles were wrapped in thick aluminium foil and placed in random order on asbestos trays in the oven to ensure that only the top surface of the sand would be heated. Five replicates of 30 seeds per crucible of each species were placed at room temperature to serve as a control.

After the scarification and stratification experiments the seeds were placed on filter paper saturated with distilled water in 9 cm plastic petri dishes in the conviron for 40 days, and subsequently treated as mentioned for the germination experiment in the conviron. After all the scarification and stratification experiments the dried fruit coat still surrounding the seed of *S. plumieri* was removed to prevent fungi infections during the germination test.

Field observations

To monitor seed germination and seedling survival in the field, belt transects of 3 m × 20 m were set out at the base of the foredunes of *I. pes-caprae* and *S. plumieri* (after Westerlaken & Maun 1985). Each transect was divided into 1-m^2 plots of which 10 were randomly chosen. In each plot the emerging seedlings were mapped and marked with colour tags, and their survival followed for 166 days. From each species 15 newly-emerged seedlings were exhumed and the length of the hypocotyl measured to determine the emergence depth.

Data analysis

For the germinated seeds of the different species a coefficient of rate of germination (CRG) was calculated (Scott et al. 1984). The data of the scarification-germination experiments of *S. plumieri* were analysed using the total number of viable seeds (all viable = germinated + ungerminated seeds) due to the fact that no seeds germinated. All statistical tests were performed using the statistical program Statistica 5.5. (Statsoft Inc., Anon. 1999). A 95% confidence interval was adopted.

Table 2. Germination response ($n = 5$) of different seed stages of *Arctotheca populifolia* (fresh + air-dry), *Ipomoea pes-caprae* (air-dry + old), *Myrica cordifolia* (air-dry + without wax), and *Scaevola plumieri* (air-dry + old) after different dry storage periods in months (age). Any seed status within a species with the same letter does not differ significantly. Contrasts obtained by the Tukey statistic after analysis by ANOVA after arcsine transformation. Level of significance: * = $P < 0.05$; *** = $P < 0.001$.

Species	Seed stage	Age (month)	Mean percentages (± S.E.)		
			Germinated	Ungerminated viable	Ungerminated dead
A. populifolia	fresh	<1	60 (1.2) b	3 (1.2) b	37 (2.3) a
	air-dry	4	47 (2.4) c	14 (2.4) a	39 (3.1) a ***
	air-dry	18	73 (2.8) a ***	18 (2.2) a ***	10 (1.5) b
I. pes-caprae	air-dry	4	1 (1.4) a	99 (1.4) a	1 (1.1) a
	air-dry	24	1 (0.3) a	97 (1.9) a	1 (1.1) a
	air-dry	36	0 (0.0) a	96 (1.4) a	4 (1.4) a
	old	>12	96 (1.8) a	0 (0.0) a	4 (1.4) a
	old	>36	95 (1.1) a	5 (1.1) a	0 (0.0) a
	old	>48	96 (0.9) a	2 (0.9) a	2 (0.6) a
M. cordifolia	air-dry	4	28 (2.9) b	68 (3.9) a ***	5 (2.3) b
	air-dry - wax	4	37 (3.8) ab	55 (3.9) a	8 (1.2) b
	air-dry	36	51 (4.7) a ***	4 (1.1) b	46 (4.5) a ***
S. plumieri	air-dry	4	0 -	100 (0.0) a *	0 (0.0) b
	air-dry	24	0 -	98 (0.8) ab	2 (0.8) ab
	air-dry	36	0 -	92 (1.0) b	8 (1.0) a *
	old	>12	0 -	99 (2.9) a *	1 (1.4) b
	old	>36	0 -	90 (1.4) b	10 (2.9) a
	old	>48	0 -	85 (2.9) b	15 (4.3) a *

Results

Germination experiment

The fresh and air-dry seeds of *Arctotheca populifolia* germinated readily, but most of the ungerminated seeds were dead (Table 2). The significant highest germination was found for the more aged air-dry seeds (ANOVA, $P < 0.001$; Table 2). The air-dry seeds of *Ipomoea pes-caprae* showed no germination but the remaining ungerminated seeds were mostly viable and even after three years in dry storage no significant loss of viability was observed ($P > 0.05$; Table 2). The 'old' seeds of *I. pes-caprae* showed a very high germination success for all seed ages (96(0.5%) with no significant decline in germination capacity or viability after different dry storage periods ($P > 0.05$; Table 2). For *Myrica cordifolia* the seeds with and without the wax layer showed no significant differences in germination success, whereas the highest germination success was found for the seeds that were kept in dry storage for three years ($P < 0.001$; Table 2). An increase in germination success after dry storage was observed, but a significant decrease in viability of the ungerminated seeds was observed after

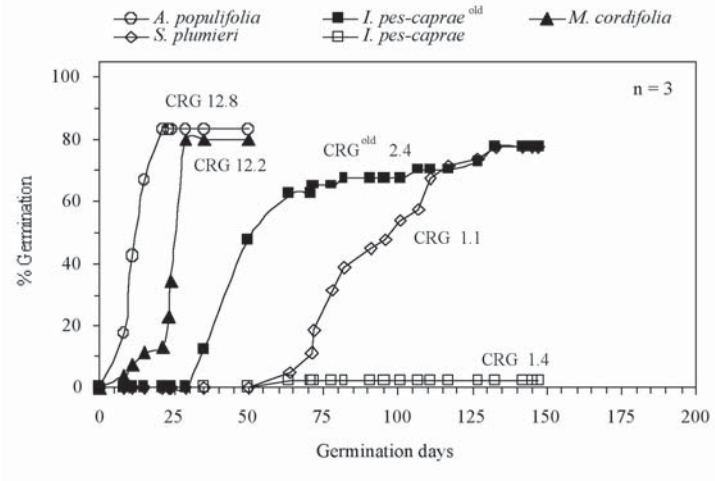

Fig. 2. Greenhouse germination of *Arctotheca populifolia* (air-dry), *Ipomoea pes-caprae* (old and air-dry), *Myrica cordifolia* (air-dry), and *S. plumieri* (air dry), with the coefficient of germination rate (CGR).

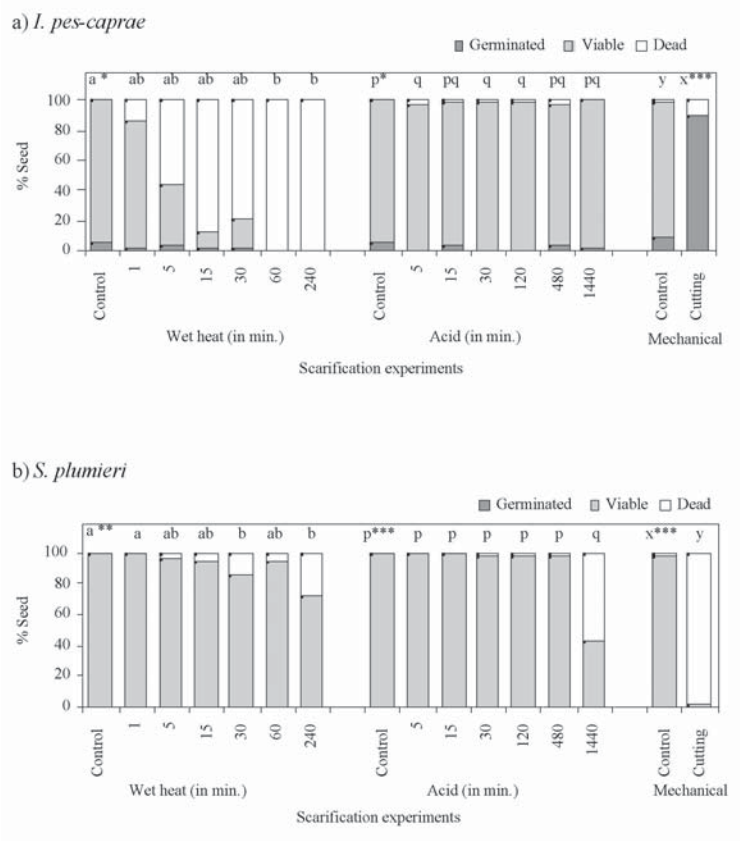

Fig. 3. Number of germinated, ungerminated viable and ungerminated dead seeds of *Ipomoea pes-caprae* (**a**) and *Scaevola plumieri* (**b**) for the wet heat, acid and mechanical scarification experiments, given per treatment ($n = 5$). Any column with the same letter does not differ significantly in percentage germinated seeds (*I. pes-caprae*) or percentage all viable seeds (*S. plumieri*). Contrasts obtained by the Newman-Keuls statistic after analysis by Kruskal-Wallis. Level of significance: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

three years in dry storage ($P < 0.001$; Table 2). The seeds of *Scaevola plumieri* showed no germination for both the air-dry and old seeds, but both seed types showed a significant decline in viability of the ungerminated seeds in the third year of dry storage ($P < 0.05$; Table 2).

In the greenhouse germination experiment seeds of *A. populifolia* and *M. cordifolia* showed maximum germination within the shortest period, resulting in a high germination rate (Fig. 2). The other species showed a much slower germination process, especially the air-dry seeds of *I. pes-caprae* (Germination Rate Coefficient, CRC = 1.4) and *S. plumieri* (CRG = 1.1) showed a long lag-phase (> 45 days) before germination, although the germination success of *S. plumieri* was high (Fig. 2). Compared to the conviron germination experiment the greenhouse germination of *A. populifolia*, *M. cordifolia* and *S. plumieri* was much higher and even the air-dry seeds of *I. pes-caprae* germinated, although the success was low (Fig. 2). In contrast the old seeds of *I. pes-caprae* showed a lower germination success compared to the germination in the conviron (Fig. 2 and Table 2).

Seed scarification

After the wet heat scarification treatments the air-dry seeds of *I. pes-caprae* showed no enhanced germination when compared to the control, but resulted in a significant decrease in all viable seeds (Kruskal-Wallis, $P < 0.001$; see Fig. 3a). After 60 min in boiling water no viable seeds were left. After the different acid stratification treatments no germination enhancement of *I. pes-caprae* seeds was observed when compared to the control, but most of the ungerminated seeds remained viable (Fig. 3a). Only the mechanical scarification resulted in a strong significant increase in germination of air-dry *I. pes-caprae* seeds ($P < 0.001$; Fig. 3a). The seeds of *S. plumieri* showed no germination after any of the scarification treatments. Although the viability of the seeds decreased after several treatments, only the 1440 min acid treatment and the mechanical scarification resulted in strong decrease in viability when compared to the control ($P < 0.001$; Fig. 3b).

Table 3. The number of germinated, ungerminated viable and ungerminated dead seeds of *Arctotheca populifolia*, *Ipomoea pes-caprae*, *Myrica cordifolia* and *Scaevola plumieri* for different stratification treatments, given per treatment (n = 5) with the Germination Rate Coefficient (CRG). Any value within a species with the same letter does not differ significantly. Contrasts obtained by Tukey after analysis by ANOVA after arcsine transformation. Level of significance: ** = $P < 0.01$; *** = $P < 0.001$.

Species	Treatment	Mean percentages (± S.E.)	Germinated		CRG	Ungerminated viable		Ungerminated dead	
A. populifolia	Control	48	(3.2) a	14		(1.4) b	40	(3.1) a **	5.52 b
	Cold	53	(2.3) a	20		(2.3) a **	27	(2.3) b	9.52 a ***
	Heat	-	-	-		-	-	-	-
I. pes-caprae	Control	6	(2.4) a	94		(2.5) a	0	(0.0) a	0.90 b
	Cold	7	(2.4) a	87		(3.2) a	6	(2.3) a	1.69 a ***
	Heat	4	(2.1) a	91		(3.1) a	5	(2.1) a	1.54 a
M. cordifolia	Control	31	(2.9) a	65		(3.9) a	5	(2.3) a	2.25 a
	Cold	39	(2.7) a	61		(2.7) a	1	(0.8) a	2.61 a
	Heat	-	-	-		-	-	-	-
S. plumieri	Control	0	(0.0) b	100		(0.0) a ***	0	(0.0) a	0.00 b
	Cold	0	(0.0) b	98		(2.0) a	2	(1.9) a	0.00 b

Seed stratification

The cold and heat stratification of the air-dry seeds of *I. pes-caprae* did not result in any significant enhancement of germination success compared to the control (ANOVA, $P > 0.05$; Table 3). Although the germination success of the control and stratification treatments was still low, a significant increase in germination rate after the cold and heat stratified seeds was observed when compared to the control ($P < 0.001$; Table 3). The seeds of *S. plumieri* showed no effect after the cold stratification, whereas a strong significant increase in germination percentage and germination rate was observed after heat stratification when compared to the other treatments ($P < 0.001$, Table 3). The germination rate was similar after heat stratification compared to the greenhouse germination (CRG = 1.1 and 1.2, respectively) (Fig. 2, Table 3). For *M. cordifolia* no effect of cold stratification was observed on germination success or germination rate, whereas for *A. populifolia* the seeds germinated significantly faster after cold stratification ($P < 0.001$), but no enhanced germination percentage was observed for cold stratified seeds of *A. populifolia* ($P > 0.05$; Table 3). Most of the ungerminated seeds of *M. cordifolia*, *I. pes-caprae*, *S. plumieri* were viable, whereas most of the ungerminated soft seeds of *A. populifolia* were dead (Table 3).

Seedling emergence and survival in the field

Due to the fact that clumps of *A. populifolia* seedlings were very scattered over the beach and foredunes, it was difficult to find seedling transects of *A. populifolia* with enough replication, whereas for *M. cordifolia* no seedlings were found. Therefore for both species no transect could be generated. For *I. pes-caprae* and *S. plumieri* numerous seedlings emerged from a depth of 6.8 ± 2.4cm and 5.4 ± 1.6cm, respectively, but not all seedlings survived (Fig. 4). The seeds of *I. pes-caprae* showed a high seedling emergence (Fig. 5), but the seedlings died almost simultaneously (Fig. 4). For *S. plumieri* the emergence and death of seedlings is more continuous when compared to *I. pes-caprae* and after 245 days 3.8 ± 0.3 seedlings per plot survived.

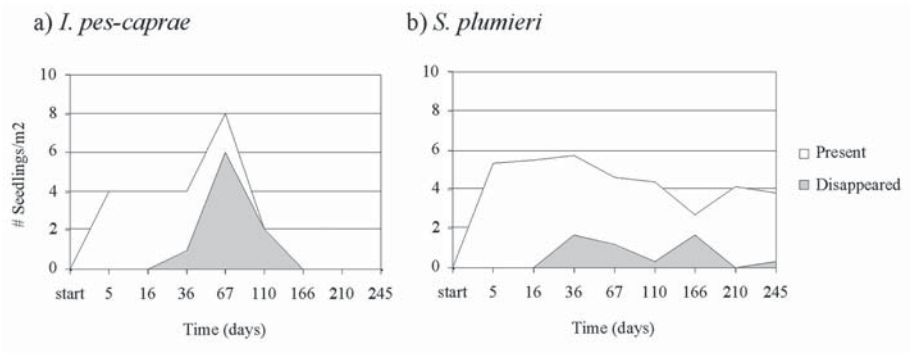

Fig. 4. Mean seedling survival (per 1-m^2 plot) in January 1999 for *Ipomoea pes-caprae* (**a**) and *Scaevola plumieri* (**b**) over the period of 245 days. Note that the x-axis is not continuous.

Fig. 5. A dense patch of even-aged 2-week old seedlings of *Ipomoea pes-caprae*.

Discussion

Some seeds of the species germinated during the present study with those of *A. populifolia*, *M. cordifolia* and *I. pes-caprae* ('old') germinating readily. The air-dry seeds of *I. pes-caprae* and *S. plumieri* germinated after scarification and heat stratification, respectively, although for *S. plumieri* the time till germination was much longer compared to the other species.

Arctotheca populifolia

The seeds of *A. populifolia* surrounded by a soft seed coat, showed a uniform pattern in germination within a short period, and the germination increased and became faster when germinated after a cold stratification treatment. This could indicate that the seeds were not subjected to dormancy, as was observed for *A. populifolia* in Australia (Heyligers 1985). On the other hand, the seeds of *A. populifolia* were four months old when germinated and the dormancy that was present in fresh seeds could have been broken during the after-ripening period during the dry storage.

The seeds of the geocarp *A. populifolia* are usually buried close to the parent plant by bending the seed-bearing flowerheads, which subsequently get buried by wind-blown sand (van der Pijl 1982; Knevel 2001). This strategy is likely to protect the seeds against predators as well as to keep the plants in the right location in an inhospitable environment (van der Pijl 1982). To germinate readily in the unstable coastal habitat is a good strategy to prevent seed predation and deep burial (Fenner 1985). The soft-coated seeds of *A. populifolia* are not capable of forming a long-term persistent soil seed bank to survive unfavourable conditions (I. Knevel & R. Bekker subm.). Therefore, fast and uniform germination is probably the only way to survive. In the field *A. populifolia* reproduced throughout the year and seedlings could be found all year round, especially after rainfall periods many seeds germinated. Resulting in clusters of even-aged seedling cohorts scattered over the strandline and foredune zone that showed a high survival (pers. obs.).

Ipomoea pes-caprae

The air-dry seeds of *I. pes-caprae* showed hardly any germination during control experiments, which was also noted for other coastal and non-coastal *Ipomoea* taxa (Gomes et al. 1978; Devall & Thien 1989; Martinez et al. 1992). The seed coat of *I. pes-caprae* is very tough, which probably prevented the seeds from germinating until the seed coat was altered physically (Bewley & Black 1994). When the air-dry seeds of *I. pes-caprae* were mechanically scarified germination improved 81%, which supports the theory that the dormancy was seed-coat induced. It is likely that the seed coat of *I. pes-caprae* is impermeable to water and gasses, which is also supported by the fact that the seeds of *I. pes-caprae* can float for months in the sea (Muir 1937).

Similar germination results were obtained with mechanical scarification of the seed coat of non-coastal *Ipomoea* species (e.g. Hardcastle 1978 – needle pricking; Devall & Thien 1989 – sand paper).

During the wet heat scarification the seed coat cracked open, revealing the embryo, as with the mechanical scarification. The embryos, however, did not survive this treatment possibly due to the high water temperature. *Acacia* seeds soaked in water of 100°C for more than 90 sec showed a strong decline in germination, whereas a treatment of 600 sec in water of 80°C resulted in high germination percentages (Teketay 1997; Thapliyal et al. 1998).

The acid scarification gave no increase in germination either, but the seeds were still viable. The sulphuric acid concentration was probably not strong enough to 'damage' the tough seed coat of *I. pes-caprae* (Gomes et al. 1978; Misra 1963). Neither could the cold or heat stratification alter the seed coat enough to break the dormancy. Due to the tough seed coat of *I. pes-caprae* seeds are protected against predators and able to survive in the soil seed bank for over 3 yr (I. Knevel & R. Bekker subm.). The long-lived character of the seeds was supported by the fact that after three years in dry storage the seeds did not show any decline in viability or germination success.

The seed coat of fresh *I. pes-caprae* seeds are covered with short dense hairs, whereas the 'old' seeds collected from the sand surface (part of the seed bank) had smooth seed coats that were thinner compared to the fresh air-dry seeds (see Fig. 1). The 'old' seeds germinated readily

with a high germination percentage, suggesting that sand abrasion might have scarified the seeds in the field (natural mechanical scarification) which made the seed coat thinner and permeable for water and/or gases (Keddy & Constable 1986; Priestly 1986; Shipley & Parent 1991). The success of the experimental (and natural) mechanical scarification indicate that the dormancy of *I. pes-caprae* was seed-coat induced (see Bewley & Black 1994). This was supported by the fact that the seeds that germinated in the field were predominantly older seeds as the hairless seed coats were still attached to the cotyledons. This supports the suggestion that the seeds were scarified due to the sand abrasion (see also Fig. 1).

The seedlings of *I. pes-caprae* started to emerge almost simultaneously within a two-week period. This explosive germination pattern was also observed for *I. pes-caprae* at the Gulf of Mexico (Devall et al. 1989). When exhumed, the newly emerged seedlings of *I. pes-caprae* showed that the seedlings could emerge from depths over 10 cm. In the dune environment the sand in which the seeds germinated dries out rapidly from the surface downwards. In order to survive, the seedlings had to maintain root elongation. Thus being large-seeded in the dune environment had two advantages for *I. pes-caprae* seedlings: shoots could emerge from greater depths and roots grew more quickly (see Fenner 1985).

Although the seeds of *I. pes-caprae* germinated and seedlings established in the field, no seedlings survived over time. This was probably due to sand abrasion in combination with heat stress and the low moisture conditions (Lesko & Walker 1969), resulting in brown leaves after which the whole seedling would desiccate. This low field survival of seedlings of coastal *Ipomoea* species was also observed by Devall et al. (1989).

Myrica cordifolia

For *M. cordifolia* the seeds germinated readily, although the germination percentage was intermediate. The low percentage could have been due to the wax layer (1.5 mm) surrounding the seed, inhibiting the water uptake, but seeds without a wax layer showed no enhanced germination success. Most of the ungerminated seeds were viable, which indicated that the seeds were dormant (see Bewley & Black 1994).

The cold stratification treatment enhanced the rate of germination, but not the germination percentage; however, when seeds were set to germinate in the greenhouse, the germination rate and germination percentage increased enormously. Perhaps the stronger fluctuations in the greenhouse and a better seed-substrate contact resulted in higher and faster germination. The seeds used were 8 months older compared to the seeds used in the conviron germination experiment. Because the seeds of *M. cordifolia* stay on the parent plant for months, creating an aerial seed bank, an explanation could be that the seeds were unripe and needed after-ripening. The extra 8 months in dry storage could have been enough time for the seeds to ripe and break the innate dormancy, resulting in higher germination success, probably because the seed coat had become more permeable when stored dry at room temperature (Egley 1979; Morrison et al. 1992). This was supported by the result that after three years in dry storage the seeds of *M. cordifolia* showed a 23% increase in germination percentage.

On the other hand the viability of the ungerminated seeds in the greenhouse decreased significantly over the same period. This could be because some unripe seeds died when dried out (Harrington 1972), the three year dry-storage period was perhaps too long for these seeds, or the right storage conditions were not met.

In the field no seedlings of *M. cordifolia* were observed. It is known that birds disperse the seeds of *M. cordifolia* (Tinley 1987) and perhaps the seeds need to pass through the digestive tract before being able to germinate in the field, but as the seeds germinated well under controlled conditions some factor(s) is (are) probably missing under field conditions.

Scaevola plumieri

The air-dry and the old seeds of *S. plumieri* were all difficult to germinate, as known from the literature (e.g. Tinley 1985; Wrigley & Fagg 1988), this in contrast to the non-dormant *Scaevola taccada* seeds that germinated readily (Lesko & Walker 1969). The seeds of *S. plumieri* germinated after 14 weeks in the conviron and a subsequent 8 weeks in the greenhouse, but with a high germination success. When the seedlings emerged in the greenhouse the seeds of *S. plumieri* were ca. 10 months old, and they germinated in the same period that the seeds would have germinated in the field. Further research is needed to examine if perhaps a certain combination of day-length and temperature is needed to trigger the seeds to break the dormancy and germinate.

The *S. plumieri* drupes were ripe when collected from the plant, but the embryos might have needed a post-dispersal after-ripening period (Pemadasa & Lovell 1975; Baskin & Baskin 1998). The seeds that had been in dry storage for 2 and 3 yr, enough time to ripen, showed the same germination behaviour.

The stone seed of *S. plumieri* is known to be very tough and able to withstand many months of submergence in seawater during dispersal (Muir 1937; Knevel. 2001), assuming that the seed coat is impermeable. As none of the scarification experiments resulted in any germination, it was unlikely that (only) a seed-coat

induced dormancy was imposed on the seed. Although the cold stratification showed no germination, the heat stratification enhanced the germination by 43% and accelerated the germination time. Although faster, the lag-phase and germination time was still much longer compared to the other species.

At the end of March the seedlings of *S. plumieri* started to emerge in the field and produced seedlings continuously in contrast to *I. pes-caprae*. This strategy was likely to be favourable in unpredictable environments because seedlings were available for establishment over a long period, preventing massive mortality due to, for instance, sand burial. Thus, the low rate of emergence due to a spread in germination time observed in the greenhouse was also observed in the field. As noted for *I. pes-caprae*, the seeds of *S. plumieri* were also large, and capable of emerging from depths over 10 cm.

In general, pioneer species produce many small seeds, but in the beach environment the pioneer species have large seeds (e.g. Fenner 1985; Barbour 1992). The large seed size could have been an adaptation to drought-avoidance by conferring on the seedling the ability to grow rapidly (Buckley 1982). Having big seeds, especially in the unstable dune habitats, could ensure successful seedling establishment. By providing an ample nutrient reserve, the seedling was enabled to reach the critical size to survive and was able to germinate to depths of more than 10 cm (Buckley 1982; Fenner 1992; Knevel 2001). The seedlings of *S. plumieri* died mainly due to saltwater inundation and sand burial. Many demographic studies indicate that even within a single species, the causes of seedling mortality may vary markedly from season to season and from place to place (see Fenner 1992), but in the unstable dune environment sand burial usually was the main cause of death (see also Tinley 1985).

Concluding remarks

The seeds of all four species germinated well when the right conditions were met and the results show that germination percentage could be increased and the germination time shortened.

For air-dry seeds of both *Ipomoea pes-caprae* and *Scaevola plumieri* a broad spread in germination over time was observed, a strategy favourable in the unpredictable coastal habitats to avoid mass mortality by producing seedlings available over longer periods.

Under controlled conditions the seedlings of all four species grew fast and showed a good survival, but this was only under ideal circumstance with enough moisture. The natural coastal environment is hostile and germinating in such a habitat is difficult.

When the four species discussed in the present study are good stabilizing species they are able to survive in the foredune environment. When these species would be used for drift sand stabilization, the success of establishment would probably be much higher if older seedlings are transplanted into the field compared to sowing of seed. Especially the seedlings of *S. plumieri* and *A. populifolia* survive well in the field. Once the vegetation is established, seed sowing could be a way of bring more plants or other species in the stabilization area as the sand movement will be lower within the vegetation and the seedlings could have a better chance to establish themselves.

However, to make the use of indigenous sand stabilizers a success, periodical and whole year round research (e.g. field trails) are needed to establish which species or combination of species will give the greatest success.

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