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The impact of introduced plants on foredune formation in south-eastern Australia

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Abstract

About one-quarter of the 50 or so plant species found on foredunes in south-eastern Australia are naturalized aliens. Several of these have become locally dominant and this prompts the following questions: Do introduced plants change the formation and shape of foredunes and, if so, to what extent are foredunes likely to lose their original character?

A description of foredune formation is given together with an overview of the foredune flora. Seven species, each of which may play a major role in building foredunes, are described in some detail. They are the native Spinifex sericeus, Festuca littoralis *and* Atriplex cinerea, *and the introduced* Cakile maritima, Ammophila arenaria, Elymus farctus *and* Euphorbia paralias. *Three examples, based on qualitative field data, illustrate the behaviour of these species in particular environments.*

From the available evidence it is concluded that:

1. *Foredunes exhibit certain physical properties which depend on the locally available species.*
2. *The introduced species important in foredune formation differ markedly from the native species in growth habit and/or response to environmental factors.*
3. *Where such introduced species are present in large numbers the morphology of the foredunes is changed.*
4. *Other coastal processes are affected as well if, due to the presence of introduced species, more sand is withdrawn from circulation in the shore zone than otherwise would have been the case.*

Introduction

"The dominant plant of the embryonic dunes, and the chief sand binder, is *Festuca littoralis,* which takes the place here of *Agropyron junceum* and *Ammophila arenaria* of the English dunes".

(Turner *et al.* 1962, p. 24)

"*Ammophila arenaria* appears to have almost totally displaced *Festuca littoralis* which was observed to occur quite rarely . . ."

(Bowden & Kirkpatrick 1974, p. 203)

Are foredune ecosystems in Australia different from those elsewhere? This question has received little attention; until recently, the remark by Turner *et al.* was the only comparison between Australian and foreign foredunes which had appeared in the literature *(vide* Doing 1985).

Foredunes are built up through the obstruction of wind-blown sand by vegetation. During this formative stage the fundamental morphology of the dunes is attained. As one may expect a long-lasting influence of this early period on later ecosystem development, an analysis of dune formation is basic to the understanding of at least some of the ensuing differences between foredune ecosystems.

European settlers in foreign lands were the first people consciously confronted with differences in sand-trapping ability of various foredune plants. In their countries of origin *Ammophila arenaria* has been used to build and restore dunes for many centuries. Consequently, when native species were found not to perform as well, *A. arenaria* was introduced to combat dune erosion. Cooper (1958) in his seminal work on the coastal dunes of Oregon and Washington, U.S.A., is the first author to draw attention to the fact that the introduction of *A. arenaria* to the eastern shores of the Pacific in 1869 has *fundamentally* changed dune building in that part of the world. Through the planting and later natural spread of this grass prominent foredunes have formed where none existed before due to the ineffectiveness of the native sandbinding species in strong wind environments. While the influence of *A. arenaria* on foredunes in Australia has not gone unnoticed, few researchers seem to have paid attention to the specific role of this or any of the other aliens naturalized along Australian shores.

This paper focuses on south-eastern Australia as most of my field work was done in that area, although it was complemented with visits to some Dutch and English dunes. Rather than assessing differences in foredune formation between Australia and western Europe, I compare species performances under local Australian conditions. This reduces somewhat the number of variables which have to be taken into account if environments as dynamic as sandy beaches are compared. The questions to be addressed are: What is the influence of various plant species on foredune formation? Do introduced species differ in this respect from native ones? If so, are foredunes likely to lose their original character?

From the outset I would like to stress that I have only qualitative observational evidence on which to base my conclusions. Hopefully, the ideas brought forward will stimulate somebody to conduct a study of greater analytical depth.

Foredunes and their formation

The term 'foredune' is used in a generic sense and covers all those sand accumulations forming through the interaction of wind, sand, flotsam

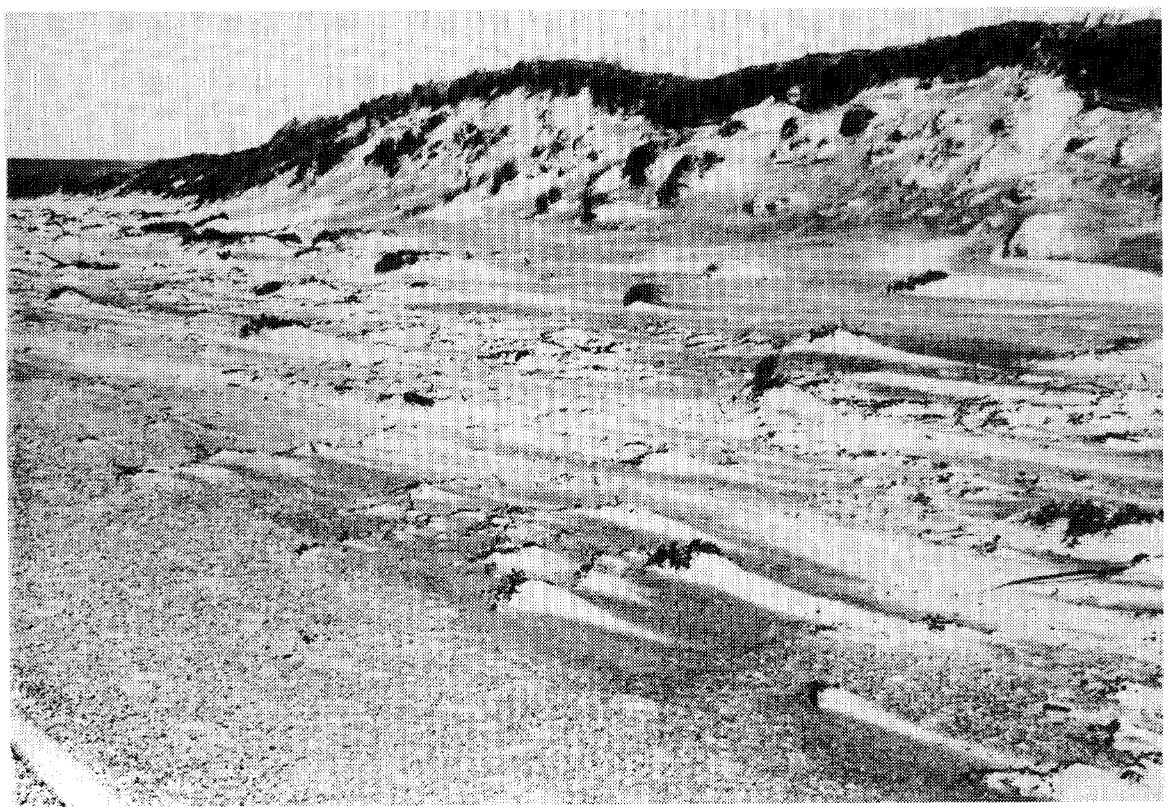

Fig. 1. The beach at Braunton Burrows, England. Shadow-dunes have formed behind strand plants including *Cakile maritima, Elymus farctus* and *Euphorbia paralias. Ammophila arenaria* predominates on the crest and frontal slope of the old dune. All four species have become naturalized in Australia and, where common, have markedly changed foredune formation.

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debris and plants on the upper part of the beach, between the high water mark and those dunes (or other landforms) where a shape has been attained which is stable and, barring catastrophic events, 'permanent'. First and foremost, the term refers to incipient dunes in the backshore zone and their development into ridges or terraces. Secondly, the term also covers those situations where the seaward slopes of frontal dunes after damage by high tides are being restored by new accumulations of wind-blown sand. In both cases plants are of crucial importance in furthering the formation and development of the foredunes (Fig. 1).

If propagules carried in by waves, wind or animals sprout and the plants are able to withstand the rigours of the backshore environment, they form nuclei for the deposition of wind-blown sand. Aeolian sand transport and the physical aspects of dune formation are well understood; Allen (1982) has adequately reviewed this subject. In contrast, the biological aspects have received only scant attention. Hesp (1981, 1982) has investigated how attributes such as plant height and width, flexibility, and shoot density, as well as plant spacing break up the wind flow and affect the size and shape of the ensuing sand accumulations. Several authors, e.g. Cooper (1958), Esler (1970), Bowden & Kirkpatrick (1974), Rosengren (1981), and Ranwell (1982), have mentioned the variations in dune form due to the presence of different plant species, but only Woodhouse *et al.* (1977) and Hesp (1982) have measured dune development over several years to document how the different dune shapes are attained.

For a substantial foredune to be built there needs to be an ample and continuous supply of well-sorted sand. Flat, wide beaches supplied with sand from longshore currents form an ideal reservoir of sediment. Even at moderate wind strengths, soon after exposure during ebb, curtains of sand grains can be seen moving over the still wet beach. Obstacles on the beach cause changes in wind force and flow, and sand precipitates where windspeeds drop below sand-moving threshold velocity. The shape of the sand accumulations is mainly

Fig. 2. Shadow-dunes building up behind tussocks of *Festuca littoralis* (foreground) and *Ammophila arenaria* (middleground) on the Shallow Inlet sandspit. Note the distinctive shape of the ridges due to species-specific differences in air flow pattern around the tussocks. The scattered shoots are from *Elymus farctus.* (The visible part of the spade handle is 0.4 m long).

determined by the kind of obstacle and the constancy of wind direction.

In physical terms, grass tussocks and other sizable upright plants are semi-porous, more or less flexible objects. Given a uniform direction of sand-moving winds, ridges will build up in their wake (Fig. 2). Although known under a variety of names, these ridges are probably best characterized as '(wind-) shadow dunes' (Bagnold 1954). The factors determining their shape have been analyzed by Hesp (1981). He found in the case of tussock grasses that width and height were largely determined by the basal width of the tussock, but length by the force of the airflow along the sides: stronger winds leave shorter wakes, hence give rise to shorter shadow dunes. Ridges will also be shorter if wind direction is variable, as eroding action due to a change in direction will be most pronounced towards the tail-end of the shadow dune. Maximum ridge height is only attained when the tussock is sufficiently tall. Otherwise, turbulence created behind the top of the tussock will interfere; the crest of the shadow dune will slope upward in the lee of the tussock and reach its highest elevation at some distance. For a given wind speed, this turbulence is diminished when the shoots are more flexible.

In contrast to tussocks and upright bushy plants, low horizontally spreading plants enlarge surface drag rather than split the air flow vertically. The resultant turbulence causes sand to precipitate in the many small wake areas amidst the leafy branches and runners.

The presence of obstacles on the backshore, however essential for foredune formation, may also initiate erosion. If objects are too dense and inflexible, the downward component of the airflow set up when the wind hits such obstacles, will not be dissipated within the confines of these obstacles as happens when less dense and more flexible objects are encountered. If this downward flow is sufficiently strong, it creates a gully along the windward side of the obstacle. Some of the eroded sand precipitates a short distance upwind, thus enhancing the size of the gully. This kind of erosion

Fig. 3. Dune mounds on the central area of the Shallow Inlet sandspit in June, 1982. In the foreground 0.5 m high hummocks formed around *Festuca littoralis;* in the distance broad mounds accumulated amongst *Elymus farctus* and about 5 m high hillocks built by *Ammophila arenaria*. The latter are the result of more than a decade of dune formation, but the *F. littoralis* hummocks are only a few years old.

TABLE 1. Some deli

Species (Family)
Ammophila arenaria (P
Elymus farctus (Poac.)
Carpobrotus aequilater
Hydrocotyle bonariens
Arctotheca populifolia
Chrysanthemoides mon
C. monilifera ssp. *rotu*
Senecio elegans (Astera
Cakile edentula (Brassi
Cakile maritima (Brass
Euphorbia paralias (Eu
Polygala myrtifolia (Po

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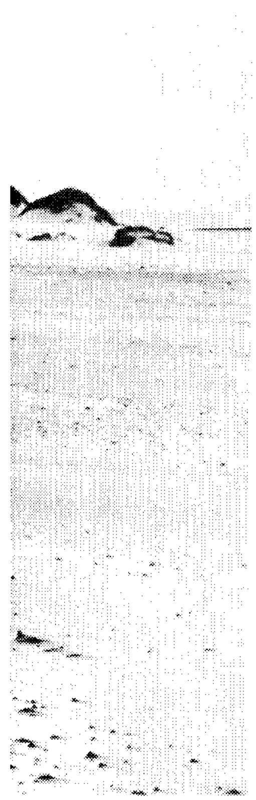

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TABLE 1. Some deliberately or accidentally introduced coastal dune plants.

Species (Family)	Origin	Date and location of introduction*	Remarks on introduction
Ammophila arenaria (Poac.)	Europe	1883, Port Fairy, Vic	Dune reclamation
Elymus farctus (Poac.)	Europe	1933, Port Phillip Bay, Vic.	With ballast?
Carpobrotus aequilaterus (Aizoc.)	S. America	1922?, Gabo Is., Vic.	—
Hydrocotyle bonariensis (Apiac.)	S. America	1902, Manly, N.S.W.	—
Arctotheca populifolia (Asterac.)	Africa	1930, William Bay, W.A. and 1937, Nelson Bay, N.S.W.	—
Chrysanthemoides monilifera (Asterac.)	Africa	1852, Sydney, N.S.W.	Ornamental
C. monilifera ssp. *rotundata*	Africa	1908, Stockton, N.S.W.	Ornamental?
Senecio elegans (Asterac.)	Africa	1857, Melbourne?, Vic.	Ornamental
Cakile edentula (Brassicac.)	N. America	1863, Phillip Is., Vic.	Vegetable?
Cakile maritima (Brassicac.)	Europe	1897, Fremantle, W.A.	With ballast?
Euphorbia paralias (Euophorbiac.)	Europe	1934, Wardang Is., S.A.	With ballast?
Polygala myrtifolia (Polygalac.)	Africa	1886, Brighton, Vic.	Ornamental

*This information, except for *A. arenaria,* pertains to the oldest preserved herbarium specimens, which do not necessarily coincide with the actual date and point of entry into Australia.

may, for instance, take place at the windward edge of a shadow dune when sand has filled the spaces between plant shoots, thus greatly reducing porosity and flexibility. When obstacles occur in close proximity, the gullies tend to become extended due to wind funnelling: acceleration of the airflow when forced to move through narrow spaces between objects.

Plants as such are not essential for the sand-deposition processes as described above. Equivalent physical objects could well be substituted. However, in the case of such objects, after sand accumulation has come into equilibrium with object shape and wind regime, no further accretion will occur, while plants through their growth provide obstructions which expand with time and continue to function as sand traps. It is the interplay between plant *growth* and sand deposition which determines the ultimate shape of the foredune (Fig. 3). This aspect is dealt with further in the next section.

The foredune-building plants

The flora of the foredunes in south eastern Australia comprises at least fifty species. About one-quarter of those are aliens which, introduced on purpose or by accident, have become naturalized (Table 1). Several of these have become prominent in the vegetation. Hence some of the earlier introductions, namely the *Cakile* species, were frequently regarded as native by twentieth century workers. The chance of finding a coastal section with foredunes carrying a vegetation exclusively consisting of native species is small indeed. Fortunately, there are still dune areas where the influence of introduced species is negligible, while other sections, where native and introduced species occur within short distances of each other, offer an opportunity for comparative studies.

Table 2 compares those native and introduced species, which appear to fulfil more or less similar roles in the dune-building process. The 'more or less' should be stressed, because the correspondence is never perfect. Moreover, it may change over time as well; for instance, while *Cakile maritima* and *Atriplex cinerea* both germinate in high tide deposits and present comparable obstacles to the wind, *C. maritima* is an annual, while the shrubby *A. cinerea* continues to grow and henceforth resembles to some degree *Ammophila arenaria* in its capacity to accumulate sand mounds.

Many of the species listed in Table 2 fulfil at best an auxiliary role in dune building, because they rarely if ever reach the density required to build ridges or terraces on their own, or else they are dune stabilizers rather than dune builders. Hence, if an assessment is to be made whether or not introduced species are essentially changing the shape and size of foredunes, attention should be focused on those species which occur in sufficient numbers to affect the outcome of the interplay between wind, sand and vegetation. *Cakile maritima, Spinifex sericeus* and *Ammophila arenaria* are the most widespread of these, while *Festuca littoralis, Elymus farctus, Atriplex cinerea* and *Euphorbia paralias* are of more local importance. With the exception of *C. maritima,* these species are perennials responding to accreting sand by rhizome or stolen extension,

TABLE 2. Some native and introduced foredune plants arranged according to comparable roles in the dune-forming process.

Native species	Introduced 'counterpart'
Drift-line pioneers	
Atriplex cinerea	*Cakile maritima*
Festuca littoralis	*C. edentula*
	Elymus farctus
Major ridge and terrace formers	
Spinifex sericeus	*Ammophila arenaria*
Other shadow-dune formers	
Senecio spathulatus	*Euphorbia paralias*
Stackhousia spathulata	
Low mound formers	
Carpobrotus rossii	*C. aequilaterus*
C. glaucescens	
Scaevola crassifolia	*Arctotheca populifolia*
S. calendulacea	
Apium prostratum	*Hydrocotyle bonariensis*
Calystegia soldanella	
Sonchus megalocarpus	
Secondary colonizers, ground-covers, etc.	
Senecio lautus	*Senecio elegans*
Lotus australis	*Sonchus asper*
Pelargonium australe	*S. oleraceus*
Epilobium billardierianum	*Conyza bonariensis*
Acaena anserinifolia	*Medicago indica*
Isolepis nodosa	
Agrostis billardieri	*Lagurus ovatus*

TABLE 3. Comparison of some species attributes by means of ranking on a five-step scale[1].

Species (*introduced)	Long-evity	Performance		Growth response to accumulating sand		Means of dispersal			Tolerance to soil salinity	
		Overall sand-trapping capacity	Vigour in cool climate	Upward	horiz-ontal	by fruits	floating capacity of fruit	veget-ative	seed-lings	older plants
**Cakile maritima*	2	3	5	1	1	5	3	1	2	4
Spinifex sericeus	4	4	3	3	5	5	4	1	1	2
**Ammophila arenaria*	5	5	5	5	3	1	2	5	1	2
Festuca littoralis	4	3	4	3	1	4	3	2	3	5
**Elymus farctus*	5	5	5	4	5	3	3	5	3	5
Atriplex cinerea	4	4	4	4	2	5	4	1	4	5
**Euphorbia paralias*	4	2	4	2	1	5	5	1	2	4

[1]The ranking has frequently been based on field evidence only; the scale ranges from 1 : attribute negligible or absent, 2 : present to some degree, to 5 : present to very high degree. Somewhat more specific are the scales for longevity (1 : annual, 2 : annual or fortuitously biennial, 3 : biennial, 4 : short to medium-lived perennial (c.25 years), 5 : long-lived perennial), floating capacity (1 : none, 2 : some days, 3 : up to 2 weeks, 4 : about 1 month, 5 : longer) and tolerance to soil salinity (1 : tolerant to up to 0.1% salt/1; 2 : 0.5%, 3 : 1.5%, 4 : 3%, 5 : > 3%).

Fig. 4. An irregular
Cakile maritima star

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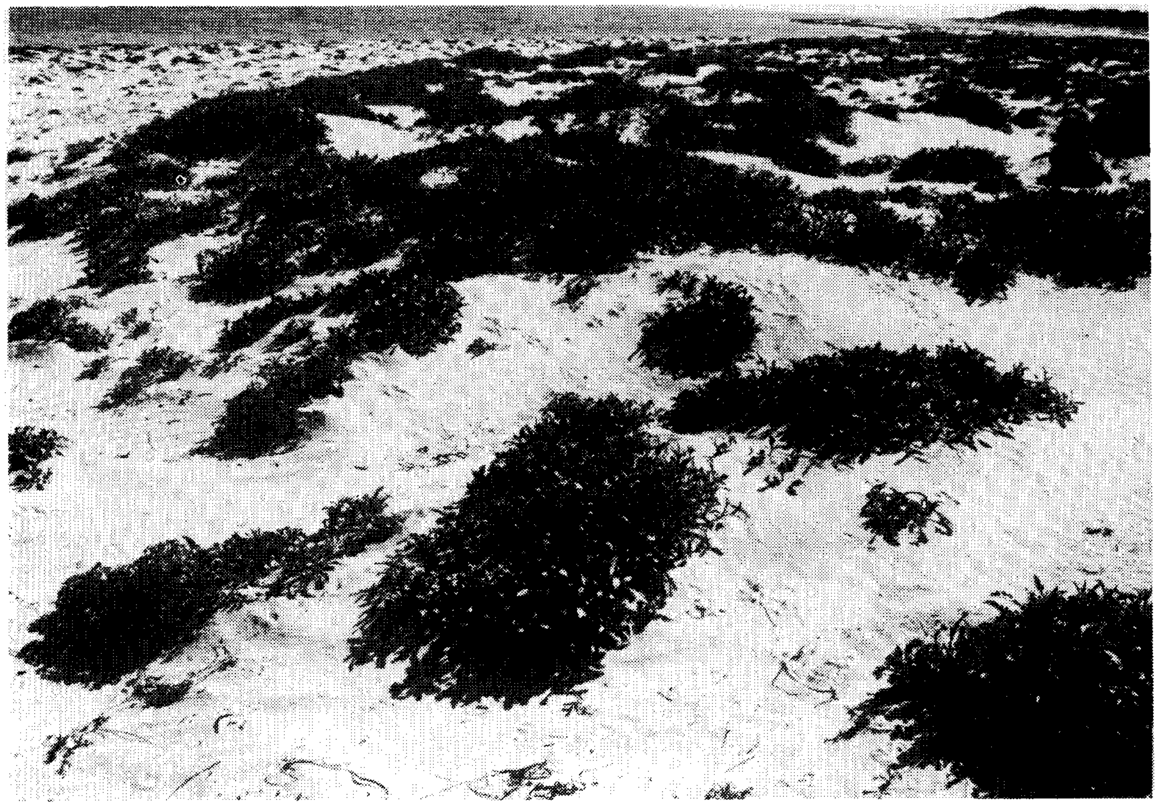

Fig. 4. An irregular foredune terrace at Cape Jaffa, built up by coalescing shadow-dunes formed in the *Cakile maritima* standline vegetation.

by shoot elongation or by shoot development from dormant buds.

The dune-building characteristics of each species are described below. Information on botanical and ecological aspects can be found in the Appendix. To facilitate comparisons between species some of their properties have been summarized in Table 3.

Cakile maritima is undoubtedly the most abundant pioneer of the upper beach. It is tolerant to salt spray, sand blast and partial sand burial, and flexible enough to withstand gale force winds. Under a fairly uniform sand-moving wind regime single plants give rise to pronounced shadow dunes. Where plants are numerous their shadow dunes merge and due to the general turbulence of the windflow caused by the unevenness in plant spacing, a foredune of irregular microrelief ensues (Fig. 4). The height attained by these incipient foredunes is largely determined by the size of the plants, but is usually less than 0.5 m.

In time a follow-up generation develops amongst the parent plants. To some degree this new recruitment compensates for the short lifespan of the parent plants by forming a continuing obstacle to the wind, but growth is seldom as vigorous and hence the new plants tend to protect the already-formed dune rather than to trap more sand.

Among the other plants which also establish on the young foredune there is likely to be *Spinifex sericeus,* originating from seeds, dropped from the infructesences blown about by the wind, or from stolons if the dune abuts an older dune with *S. sericeus* vegetation. In due course this species may become the dominant stabilizer of the new foredune.

Festuca littoralis, a tussock grass, is also a typical shadow-dune former. Because it is able to survive occasional flooding, a new shadow-dune is formed if the previous one is flattened by a high tide. Before *Cakile maritima* became widespread and predominant, incipient foredunes formed by *F. littoralis* were frequently reported in the literature (Hamilton 1917; Pidgeon 1940; Davis 1941; Turner *et al.* 1962). Such foredunes now appear to be rare; from published illustrations, their morphology resembled that of *Cakile* foredunes.

Fig. 5. The northern end of Three Mile Beach, Wilsons Promontory, with a 1 to 1.5 m high *Spinifex sericeus* foredune terrace and, further towards the headland, a 2 to 3 m high *Atriplex cinerea* foredune ridge. At the back of the terrace *S. sericeus* is invading the most southerly *A. cinerea* hillock of this ridge.

When sand deposition is slight, the tussocks become very dense. Deeper sand burial leads to shoot elongation and the formation of tufts of shoots at the new surface. However, if accretion continues, tussocks become open and shoots sparse. As *F. littoralis* rarely forms horizontal rhizomes, this fanning out of the tussocks is its predominant means to spread laterally through sand accumulations. In this way the hummocky foredune may build up in time into a ridge with a low profile and rounded crests.

Atriplex cinerea is another native colonizer of the backshore. In south-eastern Australia it is usually only a minor constituent of the strand vegetation, but it is common, or even dominant, on frontal dunes of the semi-arid coast of the western Eyre Peninsula, S.A. Single shrubs may cause low broad shadow-dunes to form but dense strandline populations may raise ridges to a height of 3 m (Fig. 5) because when branches become engulfed by sand they produce adventitious roots and extend the top growth. In this way shrubs may reach considerably larger dimensions than would otherwise have been the case. However, *A. cinerea* does not form rhizomes or root-suckers and hence lacks a means of spreading through the foredune deposits.

Elymus farctus, an introduced strandline pioneer, is different from the species discussed so far as it not only establishes from seed but also from rhizome fragments. Tolerant to a wide salinity range and occasional tidal inundation, it grows best when soil water is brackish. Once a group of tillers is formed and sand begins to accumulate between and around them, short obliquely extending rhizomes give rise to new tillers, thus greatly enhancing the sand-trapping capacity. In time, long thin horizontal rhizomes grow out from the parent plant, producing tillers when their tips emerge into the light. This enables a single plant to spread through a large area (Nicholson 1952; Gimingham 1964; Harris 1982).

Fig. 6. Beach plain of
Elymus farctus dunes,

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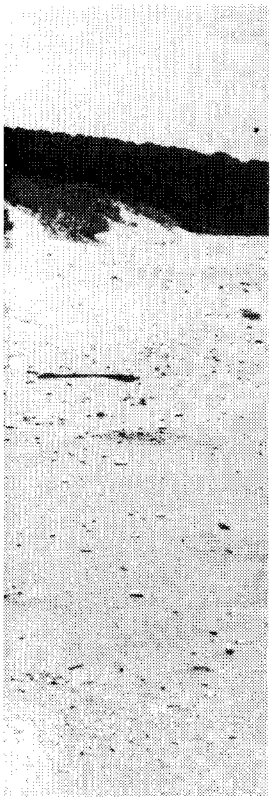

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Fig. 6. Beach plain of Schiermonnikoog, one of the Wadden Sea barrier islands, dominated by young *Elymus farctus* dunes, seen from the rim of a small blow-out, colonized by *Ammophila arenaria.*

On beach plains, under relatively moderate wind conditions, low wide foredunes are formed, the height of which is ultimately determined by the declining vigour of *E. farctus* due to the freshening of the soil water in the young dunes (Fig. 6). Exposure to strong winds tends to result in the formation of hillocks, which later coalesce into hummocky ridges or dune fields (Figs. 3 and 7). Although they are liable to wind and water erosion, when the surface cover has been damaged such hillocks remain protected by a dense mat of fibrous roots. When *E. farctus* grows along the foot of frontal dunes it builds up a fairly steep talus against the seaward slope or, if the beach is prograding, a terrace.

Spinifex sericeus, a native, and *Ammophila arenaria,* an introduced species, are dune builders par excellence. Hence, they are commonly used for dune restoration, the former in northern New South Wales and Queensland, the latter along the southern coastline where the slower growth of *S. sericeus* makes it less useful for dune repair (S.C.S., N.S.W., and S.G.A. Vic., pers. comm.). As both species need fresh soil water for optimum growth they frequently come in as secondary colonizers on foredunes started by one or the other of the species mentioned earlier.

While stolon cuttings are often used for dune restoration, under natural conditions *S. sericeus* establishes only from seed as contact with sea water kills the growing tips of the stolons (Hesp 1982). Seedlings initially form small, low, fairly open tussocks; stolons may not be produced before the following growing season, depending on growing conditions. These runners, up to 20 m long and branching only infrequently, may grow 5 cm/day or 13 m in a year (McDonald 1979; Hesp 1982). Each node bears a single shoot, but if covered by sand more shoots are formed. When deposition rates are high, these shoots grow upwards with long internodes to keep pace with sand burial.

Fig. 7. A March 1984 view along a foredune on the Shallow Inlet sandspit built up by *Elymus farctus* since 1977.

Foredunes built by *S. sericeus* often have a low, rounded profile due to the sprawling horizontal rather than vertical growth habit of this grass (Fig. 5). During periods of strong on-shore winds irregular, cusped crests are formed on these dunes due to variation in vegetation density on the seaward slope.

A. arenaria, seemingly a tussock-grass, is capable of spreading upward as well as horizontally by means of rhizomes. The 'tussocks' are in fact dense tufts of shoots formed along branching vertical rhizomes, which enable the plants to keep up with burial rates of up to 1 m/year (Huiskes 1979). While seedlings may be present in large numbers, survival rates are commonly low to nil. In Victoria this is usually due to low rainfall during the summer (S.C.A. pers. comm.). Tufts of shoots are used for planting on eroding dunes, while new growth from rhizome fragments severed from plants by storm tides and dispersed by currents is the predominant mode of natural reproduction. The sand-trapping capacity of *A. arenaria* is probably best shown by such spontaneously established plants. Higher mounds on foredune terraces dominated by *S. sericeus* are commonly formed by *A. arenaria* (Rosengren 1978), while in exposed situations, such as tombolas (Rosengren 1982) and sandspits, large, more or less isolated, 4 to 5 m tall hillocks are built up by what appear to be single individuals of *A. arenaria* (Figs. 2 and 8). Due to the strong vertical growth of rhizomes and shoots these hillocks tend to be steepsided as the sand between the shoots is often held at angles which exceed the equilibrium angle for loose sand (about 33 °).

Euphorbia paralias, introduced about 50 years ago, is generally found as a minor secondary colonizer of foredunes. Initially, stems stool out from the main stem near the root crown, later from the decumbent bases of older stems. In this manner plants are able to cope with sand accretion. Dispersal is only by seeds which may float for many months in the sea without losing their viability. Hence this species may achieve local dominance in corners of bays where flotsam has accumulated on

Fig. 8. The foredune of coalescing *Ammophila arenaria* hummocks on the East Gippsland coast opposite Gabo Island.

the upper beach. If not becoming a foredune builder in its own right, it does invade incipient foredunes and builds ridges about 1 m high (Fig. 9).

To summarize, it is likely that before the arrival of the introduced species most foredunes in south-eastern Australia were broad ridges or terraces with gentle to moderate slopes, as their formation would have been dominated by *S. sericeus,* whether or not they were initiated by *F. littoralis. C. maritima* which probably has become more common than *F. littoralis* ever was, may have enhanced the occurrence of such dunes, but has not basically changed their morphology. However, under the influence of the different growth habits of *E. farctus* and *A. arenaria,* dunes attain different characteristics if these introduced species are predominant in their formation. The following examples are used not only to illustrate this change, but also to discuss the wider impact of these grasses on local coastal dynamics.

Examples of the impact of introduced grasses

The three examples which follow are all from the northern shores of Bass Strait. Noted for strong winds, the Strait also exhibits a tidal range of about 2 m. Storms may increase the height of high water by 0.5 m and add to summer spring tides a flooding power not very different from winter tides. This means that even in summer there is no guarantee that high tides will not reach the incipient foredunes. This appears to be different from north-western Europe, where summer tides do not reach equinox and winter high water levels.

i. Foredune building on exposed beaches

When seaward slopes of frontal dunes have been undermined by storm tides, sand collects along the foot of these dunes partly due to slipping of the cliffed slopes and partly carried in by the wind from

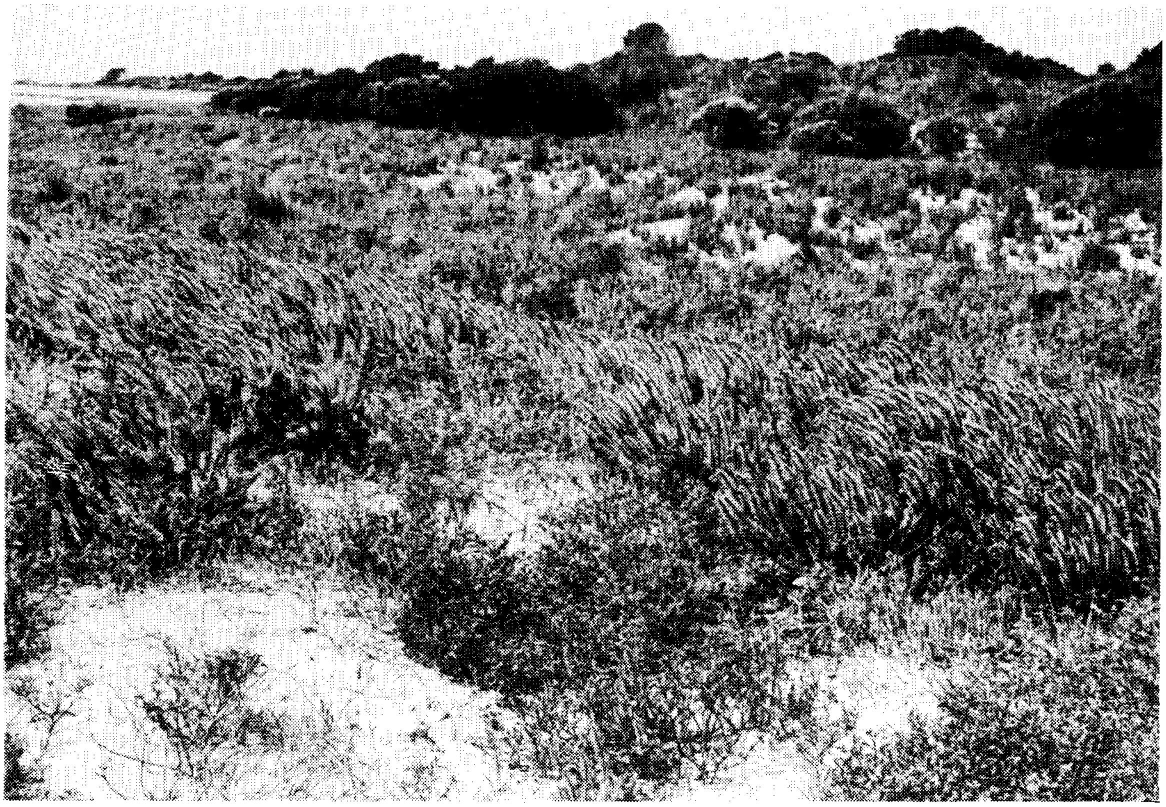

Fig. 9. Dune ridges at Cape Jaffa dominated by *Euphorbia paralias*. The younger ridge, with some *Cakile maritima* amongst the *E. paralias,* is separated by a 1 m deep swale from an older somewhat wider ridge. The shrubs of *Acacia sophorae* and *Olearia axillaris* grow in the next, shallower swale which lies in front of the older dunes with *Leucopogon parviflorus* scrub and scattered *Allocasuarina verticillata* trees.

the beach. Usually, these sand deposits are colonized by *S. sericeus* or *F. littoralis* and in time build up into terraces or low ridges. Shore sections exposed to the full impact of the south-westerlies are too severe an environment for effective performance by the native grasses (Rosengren 1981), but present conditions which are well-suited to the demands of *A. arenaria.* Consequently, this species readily colonizes such frontal dune fringes if propagules in the form of rhizome fragments or severed shoots are present. Once established, it builds substantial terraces against, or a ridge in front of, the old dune. Where beaches are wide, for instance opposite Gabo Island, numerous hillocks are formed rather than ridges (Fig. 8). Thus, owing to the presence of *A. arenaria* a significantly larger amount of sand is fixed than would have been the case otherwise. Consequently, sand supply to other areas is diminished; hence the change in local coastal dynamics extends well beyond the sections dominated by *A. arenaria.* Rosengren (1981) has discussed this with regard to the transgressive dune systems of East Gippsland.

ii. Atriplex cinerea *foredunes*

Under influence of the tidal delta current regime of Corner Inlet, some shore sections in the north-east corner of Wilsons Promontory are prograding, while others erode. On prograding sections a 'pool-and-drain' topography (Eliot 1979) develops, leading to the formation of a long linear depression behind the beach berm. After flooding during spring or storm tides this depression remains inundated for some time and under the influence of wind, flotsam is stranded along the edge. The fruits of *A. cinerea,* a frequent species along this part of the coast, are common amongst this flotsam as well as in that which was directly washed up onto the berm.

Fig. 10. Foredunes North of Hunter Point, Wilsons Promontory, with *Elymus farctus* spreading through a mound accumulated in an *Atriplex cinerea* shrub. Near the headland lies a high *A. cinerea* foredune ridge. Note towards the left the young *A. cinerea* shrubs on the backshore and, towards the right, the extensive spread of *E. farctus* in the swale.

Sand-trapping by the ensuing plant population builds up a ridge parallel to the shore (Fig. 5). In this way narrow ridges are formed, up to 3 m high, with side slopes often at sand slip angle (30°-35°). During this phase *A. cinerea* is the only species present; even when sand accumulation has reached an equilibrium commensurate with the sand-trapping potential of the shrubs, other plants are rarely found on these ridges. Only when a new ridge is being formed seaward and sand supply to the extant ridge is diminishing, do other species gradually take over: scattered individuals of *S. sericeus* and tussocks of *A. arenaria* on the frontal slope, shrubs such as *Olearia glutinosa, Acacia sophorae* and *Leptospermum laevigatum* on the leeward side.

The formation of a foredune pioneered by a shrub species appears to be uncommon. In the literature only one reference could be found, which dealt with sand drift stabilization with shrubby *Atriplex* species along the arid coast of south-western Africa (Le Roux 1974). In Europe several herbaceous *Atriplex* species occur as summer annuals in the spring equinox high water flotsam zones, but these have no lasting effect on dune development (Gimingham 1964; Moller 1975; Dijkema & Wolff 1983).

Along the east coast of Wilsons Promontory *E. farctus* and *A. arenaria* are steadily increasing their territory and the former can now be found colonizing flotsam lines together with *A. cinerea.* In areas where soil water remains brackish, *E. farctus* spreads quickly and builds low mounds around *A. cinerea* shrubs (Fig. 10). By trapping sand over a larger surface area it prevents the formation of a steep-sided ridge, hence the foredunes attain a different shape and will be subject to a different succession. As the 'take-over' by *E. farctus* appears to be recent, it is too early to foresee its likely influence. In some sections rapid sand accumulation and adverse soil mosture conditions could possibly prevent *E. farctus* from competing successfully with *A. cinerea.*

iii. Dune formation on a sandspit

About 50 years ago a sandspit began to form at the mouth of Shallow Inlet, Waratah Bay. It is still expanding due to unidirectional shifting of the inlet channel (Cecil 1983). Relatively narrow where it is joined to the older dunes, it broadens out to a plain about 1 km wide, while its total length at present is about 3.5 km. In periods between overwash long sand ripples, about 1 m high, form under the influence of prevailing winds. As far as I have been able to ascertain from aerial photographic and circumstantial evidence, the spit was still without vegetation in the early 1960s. While frequent overwash could have prevented establishment of any vegetation, it is also possible that although no native species could cope with the prevailing conditions, the arrival of *E. farctus* in the Wilsons Promontory area changed the course of events. In the late 1950s the Soil Conservation Authority used *E. farctus* in dune reclamation trials at Picnic Point, about 20 km south of the inlet (S.C.A. 1960). Four years of observations on developments on the spit together with having seen *E. farctus* in its native environment convince me that this species was the first colonizer. Brackish to salt groundwater and a covering by sand would have provided the right conditions for rhizome fragments to sprout, if such were washed up. It is significant that the first mounds which are distinguishable on the aerial photographs, were formed along the inlet shore, somewhat sheltered from the strongest winds and at a section where plant debris is frequently washed up.

In its geomorphological setting and environmental regime the spit resembles the prograding beach plains of several Wadden Sea barrier islands in north-western Europe as described by Dijkema & Wolff (1983) and Klijn (1981). During the summer the higher sections of these plains lie above the reach of normal high tides. With rain diluting the groundwater, favourable brackish conditions are provided for *E. farctus.* Once established and forming shadow dunes, its expansion is facilitated by sand ripples, which slowly move over the plains under the influence of wind. Only when dune formation is well in progress can some other species establish, for instance *Leymus arenarius* and *A. arenaria,* which form small hillocks rising above the general level of the *E. farctus* dunes. *A. arenaria* thrives especially along small blowouts initiated by storm-tide damage, where it is stimulated by the larger sand supply, while tapping the freshwater store available in these dunes (Fig. 6).

Since 1965 the foredune at Shallow Inlet has steadily developed as tidal processes continued to enlarge the spit. Now, 20 years later, this particular section of the dunes is 6 m high, 800 m long and about 200 m wide. While *E. farctus* is still dominant, *S. sericeus, F. littoralis* and *A. arenaria* have also established.

Foredunes have also formed at other parts of the spit where conditions became suitable (Fig. 7). It is noteworthy that *F. littoralis* rather than *E. farctus* has started the most recent incipient dunes. This is possibly due to the presence of what is by now a substantial seed source of *F. littoralis* on the older dunes of the spit itself. Several *F. littoralis* embryo-dunes have endured tidal overwash and develop under the same conditions as neighbouring *E. farctus* dunes (Fig. 3). This suggests that tolerance to salinity and sand burial must be rather similar for these two species, at least in this establishment phase. Hence, the question can be put: why was *F. littoralis* not the original colonizer? The species certainly occurred on the Promontory, albeit nowhere in large numbers, and I surmise that it was stranded too infrequently on the spit to establish successfully when conditions suitable for initial colonization prevailed.

In the late 1960s, while the spit grew longer and wider, some *A. arenaria* rhizomes must have found their way to the higher part. Air photos taken in 1972 show a small group of mounds about 100 m away from the *E. farctus* dune. Today, these hillocks stand as 5 m tall sentinels above the beach plains; while they gained in height, wind funnelling kept the mounds apart for many years (Fig. 3). Only recently, during a period of strong sand-ripple building, has sufficient sand accumulated in their lee to link two of the hillocks. The arrival of *A. arenaria* coincided with a period of dune restoration work by the Soil Conservation Authority at Sandy Point, about 3 km north-west of the spit, where in 1967-68 this species was planted (S.C.A. pers. comm.). It is likely that some planting material was washed up onto the spit. The possibility of this mode of dispersal was demonstrated in October 1983, when I found on a younger part of the spit, but in a very similar situation, three *A. arenaria* shoots sprouting from a buried rhizome fragment.

Young *S. sericeus* plants have only been found once or twice in the outer zone of incipient dunes of the spit and only occasionally on one year old dunes. The species occurs more frequently on older

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dunes, where it is always mixed with one or more of the other grass species, an indication of its status as secondary colonizer.

From my observations and considering the ecology of the species involved I regard it likely that in the absence of introduced grasses the spit would eventually have been colonized by *F. littoralis,* with *S. sericeus* establishing later in the incipient dunes, and that in time a dune with a low profile would have been formed. However, due to the arrival of *E. farctus,* dunes were initiated earlier and attained much greater heights than otherwise would have been the case. Consequently, a greater quantity of sand has come to rest on the spit. When the inlet was surveyed in 1841, the spit was mapped as 'drift sand'. Since this first survey the spit has been destroyed and rebuilt at least once and possibly twice due to cyclic changes in the position of the tidal channels (Smith 1968; Cecil 1983). I have found no evidence to assume that there was vegetation on the previous spits. Old photography shows a wide expanse of sandy shoals and, to the south-east, a sandy flat beyond the channels when these lay close to the old dunes of Sandy Point. In view of the large amount of sand presently accumulating the spit, it is quite likely that when the next breakthrough occurs at the neck, the spit will not be totally destroyed as seems to have happened on previous occasions, but that the dune area will remain as an island.

Discussion and conclusion

To assess whether or not introduced plants build foredunes different from those formed by native species, it should be recalled that already the shape of a shadow dune bears the imprint of the plant type, if not the plant species, behind which it is formed: from sharp-crested and narrow-based behind grass tussocks to flatter and wider behind spreading plants, due to the different manner in which the windflow is broken up. Hence, in the colonizing backshore vegetation the dominant growth form largely determines the shape of the embryonic dunes, and if an introduced species differs in that respect from a native one, the incipient dunes will be different in form. As the most widespread introduced grass, *Ammophila arenaria,* is a tussock former, and the most common native grass, *Spinifex sericeus,* a spreading plant, the embryonic foredunes built by either of these have different shapes.

The other attribute equally important in shaping foredunes is plant response to accumulating sand. In this respect the introduced *Elymus farctus* and *A. arenaria* generally surpass the native grasses, largely due to their capability to produce fast-growing horizontal and/or vertical rhizomes. *S. sericeus* reacts to sand burial by stolon and shoot extension, apparently a slower process than rhizome growth, at least under south-east Australian conditions, while *Festuca littoralis* lacks an efficient means of horizontal extension. Hence, more sand is trapped by the introduced grasses than the native ones, with the result that they have the capacity to form larger foredunes.

The other aspect to be discussed is the capability to initiate foredune formation once propagules have reached the backshore. Tolerance to high substrate salinity levels will be the principal factor determining germination and seedling establishment. In this respect there are native as well as introduced species, which show tolerance to such conditions: *Atriplex cinerea, F. littoralis, Cakile maritima* and *E. farctus.* While especially in the older literature *F. littoralis* is usually mentioned as the most important colonizer of the backshore, at present *C. maritima* is commonly the species which dominates on the incipient foredunes. Under very extreme conditions, combining high soil salinity and exposed location, *E. farctus* appears to be the only species able to establish. This and the ability to spread quickly through accumulating sand makes *E. farctus* a colonizing species without equal amongst the native flora.

In summary, one is lead to the conclusion that the introduced grasses and herbs are more efficient than native species at colonizing the backshore and in trapping sand. Due to their presence, therefore, either foredunes are formed where none would have come into existence otherwise, or the formation of foredune terraces and ridges is enhanced and larger dunes are built up as a result.

The degree to which size and shape of a foredune are affected when an all-native pioneering plant assembly gives way to one in which introduced species occur as well, depends on the particular species and the numbers in which they are present. Their effect may be negligible or transient, e.g. in the case where *S. sericeus* becomes dominant on a foredune terrace formed by *C. maritima.* On the other hand, when either *E. farctus* or *A. arenaria* is the main constituent of the vegetation, their imprint will be long lasting as the morphology of the dunes they build is different from that of the dunes formed by the native species.

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Appendix

The aim of the following abridged descriptions of the more important foredune-building species is to introduce available botanical, biogeographical and autecological literature. Only some gaps I have endeavoured to fill in with my own observations. References given after the botanical name in the opening paragraph for each species refer to taxonomic treatments. The order in which the species are described reflects their ubiquity in south-east Australia, especially Victoria.

Cakile maritima Scop. (Hewson 1982; Rodman 1974) is an often much-branched bushy annual or opportunistic biennial with rather succulent, more or less deeply dissected leaves and usually pinkish-purple flowers. The fruits consist of two segments, each containing one seed. The mature upper segment dislodges easily, the lower remains firmly attached to the stem. Plants have no means of vegetative reproduction, nor do they develop adventitious roots.

Native to western Europe and the Mediterranean, *C. maritima* reached Australia late last century. In Victoria it has replaced *C. edentula,* a process which is still going on along the coasts of New South Wales and, possibly, South Australia (Rodman 1974; Heyligers 1984).

Plants are not affected by salt spray and tolerate brackish groundwater, while shoot growth is greatly stimulated by high light intensity (Barbour 1970). Also, plants respond to nitrate over a wide range of concentrations (Garcia Novo 1976).

Buoyancy experiments with upper fruit segments have repeatedly shown that these will float in seawater for only about 10 days at best. After about 6 weeks submersion germination is reduced, but some seeds are still viable after three months (Rodman 1974). Once germinating, soil water salinity should be about one third or less of that of sea water in order not to inhibit growth of the seedlings (Ignaciuk & Lee 1979).

Dispersal is also effected by birds. Rosellas *(Platycercus* spp.) and migrating Orange-bellied parrots *(Neophema chrysogaster)* (Brown & Wilson 1982; Brown 1984) eat the seeds. Emus *(Dromaius novaehollandiae)* graze the plants; they pick off whole branch tops, whether or not in fruit (Heyligers 1984). *Cakile* is likely to be a valuable green feed as in 'the olden days' it was well-known for its antiscorbutic qualities (Rodman 1974). While dispersal by parrots is not proven, seedlings emerging from skats show the effectiveness of emus as a dispersal agent.

Spinifex sericeus R.Br. (Craig 1984) is a perennial grass with strong stolons, which root at the nodes. Leaves crowded near the base of the shoots, densely covered with short silky hairs. Blades about 30 cm long and 8 mm wide, flat or more often inrolled to a certain degree. Plants are either male or female; the female inflorescence is a terminal cluster of sessile spikelets, each supported by a tightly inrolled bristle-like bract, 10-15 cm long. On maturity it is dislodged and rolled along by the wind.

S. sericeus ranges from north-eastern Queensland to the south-east of South Australia. It also occurs in New Zealand, especially on North Island, and in New Caledonia. Germination and growth requirements have been experimentally determined by Harty & McDonald (1972), McDonald (1979), Maze (1982), and the Beach Protection Authority of Queensland (1980, 1983). Hesp (1982) has followed the life-cycle in the Myall Lakes region, N.S.W. He never found seedlings amongst established *S. sericeus* vegetation, always in swash deposits, either contiguous with the earlier formed foredune or further down the beach, where they may initiate a new foredune ridge. Plants found on foredunes formed by *Cakile* and other mound-building species, are more likely to have grown from wind-dispersed rather than from sea-borne seeds. Apparently, there is no experimental evidence on tolerance to groundwater salinity. Also, little information is available how *S. sericeus* copes with sand deposition. Investigating the possibility that short term accretion would induce more shoots to be produced, Hesp (1982) found no apparent correlation between the amount of accumulated sand and numbers of shoots.

Ammophila arenaria (L.) Link (Tutin 1980) is an erect perennial rhizomatous grass, up to 120 cm high. The 'tussocks' are dense tufts of shoots formed along branching vertical rhizomes. Leaf blades are inrolled, fairly stiff but flexible, with a conspicuous, c. 2 cm long ligule. The dense cylindrical panicles are borne on stems taller than the leaves.

Originally, its distribution was confined to the coastal sand dunes of Europe and North Africa between the latitudes of 30° and 63°N, but it has been introduced into other temperate areas for dune stabilization, e.g. in 1883 into Victoria to fix the sand drifts in the Port Fairy area (Maiden 1906). Planted or spontaneous, *A. arenaria* can now be found in south-western Western Australia and from the Eyre Peninsula, S.A. to southern Queensland. For a recent review of the biology of this species the reader is referred to Huiskes (1979).

Festuca littoralis Labill. (Vickery 1939) is a perennial, seemingly tussock-forming grass; tufts of shoots, however, arise from a short branching vertical rootstock. Leaf length varies from about 20 to 50 cm, depending on growth conditions. Blades are narrow, usually rightly inrolled and their tips sharp-pointed. The ligule is a stiff, short protrusion from the sheath. The length of the flowering shoots is variable and the dense spike-like panicles may or may not overtop the leaves.

F. littoralis occurs from the Central Coast, N.S.W., to the west coast of the Eyre Peninsula, S.A., in the south-west of Western Australia and in New Zealand, including Stewart Island. According to Zimmerman (1980), in South Australia it "grows best under steadily accumulating sand on frontal dunes and transgressive dunes". Mature panicles persist for a long period, providing ample opportunity for the seeds, ensheathed in glumes, to be shaken out by the wind (Zimmerman 1980). No observations are available on long-range seed dispersal, but apart from wind, water is the other obvious dispersal agency. I surmise, that dispersal could also happen by vegetative means: erosion sometimes exposes the tufts developed at the end of the short rootstocks; if these tufts break loose, they may be spread by wind and water in a way similar to *S. sericeus* heads. Seedlings and young tussocks can be found on the

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upper beach, within reach of king tides, and this suggests that *F. littoralis* is tolerant to brackish groundwater and can withstand occasional inundation by sea water.

Elymus farctus (Viv.) Runemark ex Melderis (Melderis 1978, 1980), formerly known as *Agropyron junceum,* is a rhizomatous, sward-forming grass. The glabrous blue-green leaves are almost flat, c. 25 cm long and 5 mm wide, but inrolled and smaller when plants grow under unfavourable conditions. Flowering culms are stiffer than vegetative shoots. At maturity, the inflorescences readily break up, enabling the fruits to be scattered by the wind. No data appear to be available on seed longevity or on the floating capability of 'fruits'. Vegetative reproduction occurs by means of severed rhizome fragments (Harris 1982).

E. farctus is indigenous to the shores of Europe. Its original introduction into Australia seems to have been accidental; it was first collected at Port Phillip Bay in 1933. Its present range extends from the eastern shores of Bass Strait to Lacepede Bay, S.A.

Harris (1982) has found that virtually all seeds germinate when only shallowly buried, but that percentage germination decreases with increasing depth and is nil when depth exceeds 15 cm. Nicholson (1952) ascertained that germination is completely inhibited by sea water and reduced by any salt concentration exceeding 0.5%. Mature plants tolerate a wide range of salt concentrations, up to twice that of sea water, but perform best when soil water is brackish, i.e. betwen salt concentrations of 1.6 and 2.4% (Meijering 1964).

Atriplex cinerea Poir. (Wilson 1984) is a low-branching shrub, up to 2 m tall and 4 m across but may reach considerably larger dimensions when engulfed by sand. The grey, scale-covered, somewhat succulent lanceolate leaves are c. 4 cm long. Male and female inflorescences are usually borne on different plants. Two corky bracteoles surround each fruit and provide the vehicle for dispersal by sea. Vegetative reproduction, either from severed branches or from roots, is apparently absent. It occurs from the North Coast, N.S.W., to the west coast of Western Australia.

No experimental information is available on the autecological requirements of *A. cinerea.* At Cape Schank, Vic., it has recently been used for planting on reclaimed carparks and, amongst hay-mulch, on eroded headland slopes. Although soil conditions at these sites are quite different from those of the foredunes, the nursery-raised plants generally perform satisfactorily (National Parks Service, Vic., pers. comm.). In the south-west of Western Australia it is being tested as a forage species for salt-affected soils, as it is particularly palatable; the preliminary results have shown considerable promise (W.A. Department of Agriculture, pers. comm.).

Euphorbia paralias L. (Smith & Tutin 1968) is a caespitose perennial herb; clumps may be up to 1 m tall and reach a spread of 1.5 m. Initially, stems stool out from the main stem near the root crown, later from the decumbent bases of older stems. In this manner the plant is able to cope with sand accretion. Spring and autumn are the main growth periods and frequently three generations of shoots can be seen on a single plant. The somewhat fleshy leaves are glabrous, glaucous but often tinged with red, and up to 3 cm long.

The terminal inflorescence is an 'untidy' umbel. Each fruit contains three seeds and when ripe its dry wall breaks apart, releasing the 3 mm globular seeds. Seeds stay afloat for several weeks, and some much longer, without losing their viability (Guppy 1906; Heyligers unpubl.). Also, wind can roll the seeds over bare surfaces for long distances as shown by seedlings growing at the foot of sand-drift slip-faces hundreds of metres inland from the beach. However, the large number of seedlings which can often be found in the immediate vicinity of parent plants indicate that seed dispersal is frequently quite limited.

E. paralias is indigenous to western Europe and the Mediterranean (Tuxen 1975; Bakker 1976). In Australia it was first collected in 1934 on Wardang Island, S.A. P. M. Kloot (pers. comm.) surmises that it "was almost certainly introduced with ballast dumped from the nearby Port Victoria at which ketches were loaded". Now, 50 years later, its range extends from King George's Sound, W.A., to Flinders Island in Bass Strait and there is no reason to suppose that it has reached its limits.

There do not appear to be any experimental data on the environmental tolerances of *E. paralias.* My field observations suggest that it is quite drought-resistant and can withstand wide fluctuations in groundwater salinity. Also, that it is tolerant to, and probably benefits from, partial burial by driftsand.