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Source: Journal of Coastal Research, 2005(211) : 175-185

Published By: Coastal Education and Research Foundation

URL: https://doi.org/10.2112/01041.1

Journal of Coastal Research	21	1	175–185	West Palm Beach, Florida	January 2005

Processes of *Ammophila arenaria* (Marram Grass) Invasion and Indigenous Species Displacement, Stewart Island, New Zealand

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ABSTRACT

HILTON, M.; DUNCAN, M., and JUL, A., 2005. Processes of *Ammophila arenaria* (marram grass) invasion and indigenous species displacement, Stewart Island, New Zealand. *Journal of Coastal Research,* 21(1), 175–185. West Palm Beach (Florida), ISSN 0749-0208.

The present study (1) describes the rates and patterns of *Ammophila arenaria* (marram grass) invasion in a large transgressive dune system (Mason Bay) and on a prograding foredune-ridge barrier (Doughboy Bay), Stewart Island, New Zealand; (2) examines the impact of *Ammophila* on dune morphology and indigenous dune biota; and (3) assesses the significance of geomorphic processes in accounting for the patterns observed. Processes of *Ammophila* invasion are interpreted from evidence of landform development and vegetation change; field observations and survey of dune landforms and dune vegetation; the aerial photographic record and historic accounts of the local botany.

The area dominated by *Ammophila* in the Mason Bay study area has increased from 1.4 ha in 1958, to 17.8 ha in 1978, to 74.9 ha in 1998; a 5,204 percent increase. *Ammophila* invasion of active dune systems in the study areas is clearly associated with dune forming processes—shadow dune development; migration of long-walled parabolic dunes; stoss face blowout development; and barrier progradation. The primary mechanism of native species displacement appears to be burial rather than competition for nutrients. *Ammophila* traps sand and builds dunes at rates that may exceed the threshold of tolerance of local native species. *Desmoschoenus spiralis,* the dominant indigenous foredune species, cannot co-exist with *Ammophila* in the active dune systems investigated.

ADDITIONAL INDEX WORDS: Desmoschoenus spiralis*, foredune complex, parabolic dune migration, Mason Bay, Doughboy Bay, burial, shadow dune.*

INTRODUCTION

Ammophila arenaria (Marram Grass or European Beachgrass) has been introduced to the active dune systems of southeast Australia (HESP and THOM, 1990; CULLEN, 1998); North America (WIEDEMANN and PICKART, 1996); South Africa (HERTLING and LUBKE, 1999a); Chile (HULTEN and FRIES, 1986; CASTRO, 1988) and New Zealand (JOHNSON, 1992; PARTRIDGE, 1992). At most sites it has been planted to construct or re-establish foredunes or stabilise transgressive dune systems.

Ammophila has belatedly been shown to be highly invasive and a threat to the ecology of active dune systems outside its natural range. It may adversely affect indigenous dune flora and the diversity of habitats by stabilizing naturally mobile dunes and accelerating vegetation succession (COOPER, 1958; BUELL, PICKART and STUART, 1995; HERTLING and LUBKE, 1999b). The area of bare sand, species diversity and evenness (uniformity in abundance and cover of species) has been shown to correlate negatively with *Ammophila* along the west coast of the United States (reviewed by PICKART and SAWYER, 1998) and in Tasmania (reviewed by CULLEN, 1998).

01041 received 3 May 2001; accepted in revision 25 July 2002.

To date, the processes of *Ammophila* invasion and indigenous plant displacement have only been described in general terms. For example, BUELL, PICKART and STUART (1995, p.1591) attribute the rapid and successful spread of *Ammophila* through the dunes of North Spit, Humboldt Bay, California, to "a number of processes and conditions: optimal habitat, multiple introduction, natural and human disturbance, and proximity to the strand where rhizome fragments are washed ashore by storm surf". Increasing our understanding of these processes will assist conservation agencies assess the vulnerability of dune systems to *Ammophila* invasion and increase the effectiveness of *Ammophila* eradication operations.

The impact of *Ammophila* on the native dune flora and fauna of New Zealand has been recognised for some time (*e.g.* JOHNSON, 1992; DEPARTMENT OF CONSERVATION, 1997). New Zealand has three indigenous foredune sandbinders, *Desmoschoenus spiralis* (a sedge), *Austrofestuca littoralis* (a perennial grass) and *Spinifex sericeus* (a perennial grass). *Desmoschoenus* and *Austrofestuca* occur throughout New Zealand while *Spinifex* occurs throughout the North Island and in northern South Island. *Ammophila* has displaced *Desmoschoenus* in many dune systems, but particularly around the south and east coasts of the South Island and the exposed western coasts of the three main islands. *Ammophila* is almost the only foredune species on exposed western coasts and around the south coast of the South Island of New Zealand. A recent inventory of threatened plant species in New Zealand concluded *Ammophila* was a threat to ten indigenous dune species, including *Desmoschoenus* and *Austrofestuca* (REID, 1998).

The displacement of indigenous dune plant species in mobile dune systems appears to be related to geomorphic processes of dune development. *Ammophila*-dominated dunes are generally steeper and higher than dunes formed in association with the indigenous foredune species, *Desmoschoenus spiralis* and *Spinifex sericeus* in New Zealand (ESLER, 1970; HOLLAND, 1981). PARTRIDGE (1995) concluded *Ammophila* can either co-exist with *Desmoschoenus* or displace it, depending on several factors. The species can co-exist in three situations: (1) on the front of the foredune where marram grass spread is limited by high salt concentrations; (2) where moisture in the upper sand layers is not limiting; and (3) where both species are moribund because of low rates of sand accumulation. Displacement of *Desmoschoenus* was found to be most severe on stable dunes and where moisture in the upper layers of sand was limiting. *Desmoschoenus* displacement was found to be unrelated to the form and geomorphic processes of different kinds of dunes.

The process of *Ammophila* dispersal and invasion in active dune systems is not well documented in New Zealand, partly because most dune systems were completely occupied by *Ammophila* by the mid 1900s. Specific geomorphic conditions that aid or hinder *Ammophila* invasion have not been described. The present study (1) describes the rates and patterns of *Ammophila* invasion at two sites on the west coast of Stewart Island, New Zealand; (2) evaluates the importance of geomorphic processes in accounting for these patterns; and (3) interprets the rate and processes of *Desmoschoenus* displacement by *Ammophila*.

STUDY AREAS

Mason Bay

The combination of available sediment and prevailing onshore winds has led to extensive dune building and transgressive dunefield development along the western and northern coasts of Stewart Island. Prevailing winds are from the west (Figure 1). The active dune systems of Stewart Island encompass a range of primary and secondary dune forms in a variety of depositional environments. Mason Bay contains the largest transgressive dune system on Stewart Island and one of the largest and least modified dune systems in New Zealand. Between Martin's Creek and Duck Creek, the active dune system extends up to 3 km inland. The foredune complex is a large, continuous feature up to 15 m high and 150 m wide. Landward of the foredune a series of active U-shaped, long-walled parabolic dunes (after PYE, 1983; HESP and THOM, 1990) are transgressing a broad, gently-sloping stonefield. These dunes are evident in 1958 aerial photographs and formed prior to the arrival of *Ammophila* in the central area of Mason Bay. The hinterland of the dune system north of Martin's Creek to the northern end of the Mason Bay dunefield is dominated by parabolic dune forms. *Ammophila* was planted near Kilbride at the southern end of Mason Bay in the early 1930s (Figure 1) and east of the 'Homestead' in the mid 1960s (Figure 2). *Ammophila* now dominates the foredune environment but is patchy and present in very low densities across approximately 60 per cent of the hinterland of the active dunefield between Martin's Creek and Duck Creek. *Austrofestuca littoralis* and *Desmoschoenus* remain the primary sandbinders landward of the stonefield.

Doughboy Bay

The active dune systems of Doughboy Bay provide opportunities to study processes of marram grass invasion on a rapidly prograding bay-head barrier. Until recently the series of foredune ridges that comprise the seaward half of the southern barrier had not experienced significant disturbance. These are primary dune forms that have developed in conjunction with *Ammophila*. The foredune ridges formed since the 1960s, probably as a result of post-storm sedimentation.

METHODS

Patterns of *Ammophila* Invasion

The distribution and density of *Ammophila* in the Mason Bay study area were mapped from vertical aerial photographs flown in 1958, 1978 and 1998. The 1958 photographs are relatively poor black and white images, but of sufficient quality to allow the identification of areas of *Ammophila*. The remainder are high quality colour images, printed at 1:3,000 and 1:10,000. Resolution of contrasting features is approximately 1 m^2. The southern dune system of Doughboy Bay was photographed in 1977, 1987 and 1999. The 1977 Doughboy image is also black and white. Maps of *Ammophila* distribution and density derived from the 1998 (Mason Bay) and 1999 (Doughboy Bay) aerials were field checked during 1999.

Maps of the location and density of *Ammophila* between Duck Creek and Martin's Creek were constructed using ARC/INFO software. The 1:3,000 1958 image was digitised by hand. The 1978 and 1998 images were scanned at 1:10,000. This permitted on-screen digitising of these images using the 1:3,000 images for reference. All Mason Bay maps were ortho-rectified based on GPS observations of distinctive features.

Five density classes of *Ammophila* were mapped in the Mason Bay study area (0–5, 6–25, 26–50, 51–75 and greater than 75 percent). Classes refer to the proportion of ground covered by *Ammophila* within discrete areas. These areas generally correspond with the boundaries of particular landforms, for example, the depositional lobes of parabolic dunes. *Ammophila* is considered the 'dominant' species where it comprises more than 50 percent ground cover within a discrete area. Just one density class is recognised at Doughboy Bay (>50 per cent). *Ammophila* occupied 100 percent of the active dune system seaward of the storm scarp in 1977 at densities exceeding 50 percent ground cover.

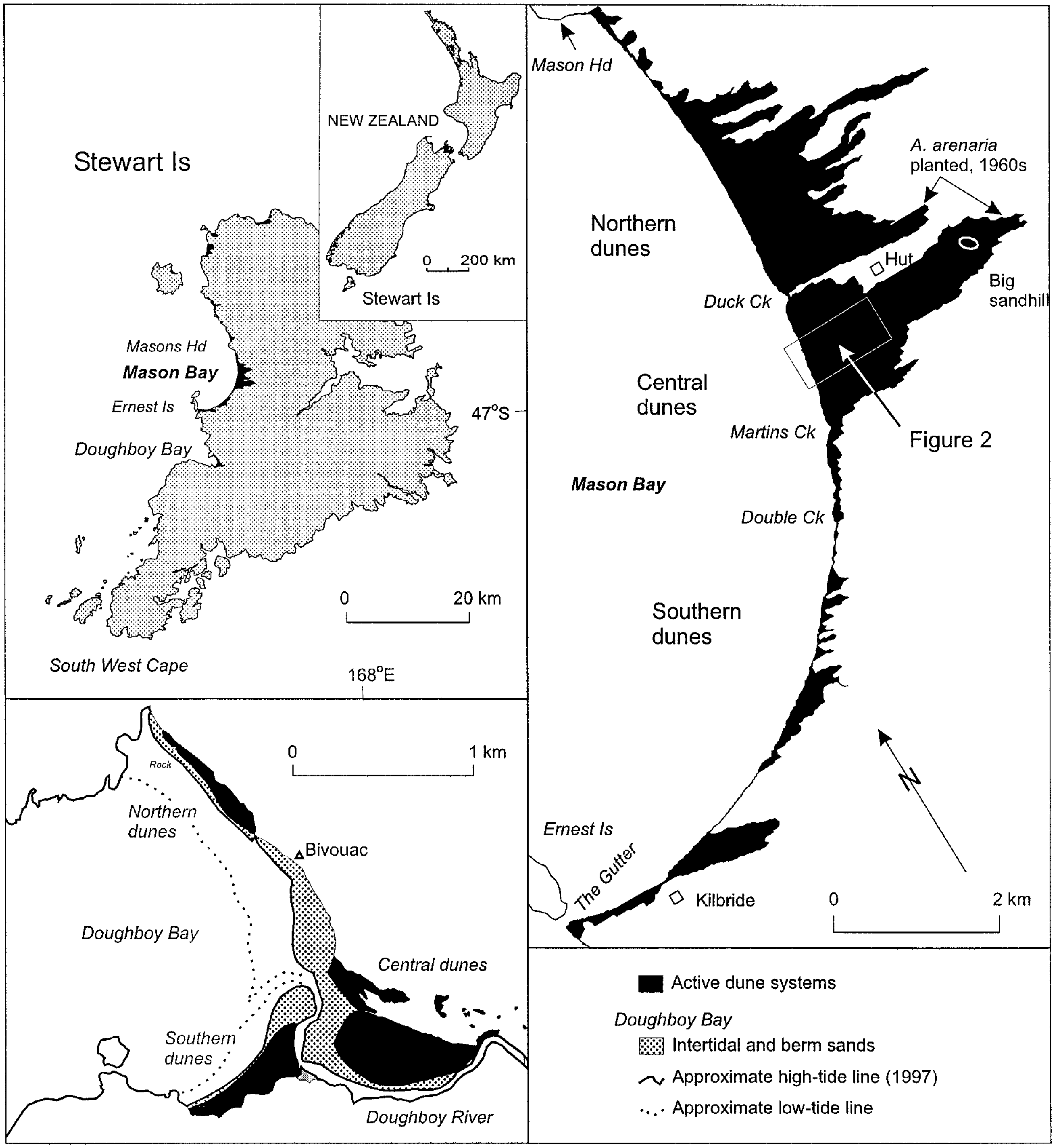

Figure 1. Location of study sites and major Stewart Island active sand dune systems. Wind rose derived from hourly observations, Southeast Cape, Stewart Island (1992–97).

Landform Development and Vegetation Change

Contemporary vegetation cover in the Mason Bay study area was estimated by random sampling (1 m² quadrat) in January 2000. The quadrat data was then stratified into five classes based on geomorphic characteristics: (i) the stoss face of foredune complex (40 sites); (ii) the lee slope of the foredune complex (40); (iii) the deflation zone of the long-walled parabolic dunes (40); (iv) trailing arms (40); and (v) depositional lobe (25). The average ground cover for each stratum was derived by averaging the percent cover of the major species observed in each quadrat. Our interpretation of species diversity at Doughboy Bay is based on data gathered over a three year period (1999–2001) from ten permanent quadrats

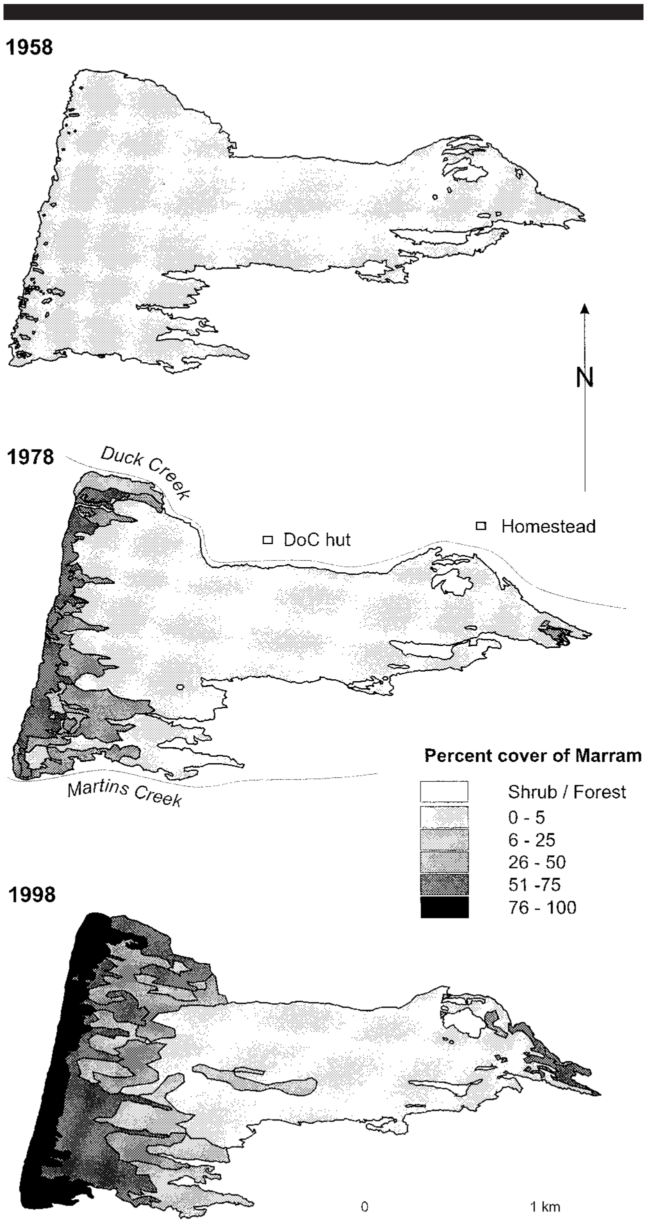

Figure 2. *Ammophila arenaria* invasion of Mason Bay study area, 1958–1998, based on aerial photography interpretation. Only the 1998 pattern was field checked.

located across the *Ammophila*-dominated section of the southern dune barrier (which comprises about half of the total area of the barrier). These quadrats were established to monitor vegetation change during an *Ammophila* eradication programme, which commenced in January 1999.

Historic vegetation cover (1908–present) and associated landforms were interpreted from aerial photographs, a survey of dune landforms and dune biota (including dead plant material, especially *Desmoschoenus* root material); and early botanical accounts. Leonard Cockayne, one of New Zealand's pioneering botanists, described the dunes and dune flora of Mason Bay in 1908, prior to the introduction of *Ammophila* (COCKAYNE, 1909). In addition, *Ammophila*-dominated foredunes in the Mason Bay study area were compared with remnant foredunes in northern Mason Bay. *Desmoschoenus* is still the primary sandbinder along small stretches of coastline north of Duck Creek and is the dominant sandbinder across large areas of the hinterland.

RESULTS

Patterns of *Ammophila* Invasion

Ammophila spread north in Mason Bay following introduction at Kilbride by farmers in the 1930s. By 1958 *Ammophila* had established a small number of dense colonies north of Martin's Creek (Figure 2). The total area of dense *Ammophila,* where *Ammophila* cover exceeded 50 percent, was around 1.4 ha. At that time almost all *Ammophila* occurred within 400 m of the toe of the foredune. Further north, beyond the advancing *Ammophila,* the foredune comprised a band of low shadow and/or coppice dunes, approximately 40 m wide. The indigenous foredune vegetation in 1958 was sparse (comprising, perhaps, 10–30 per cent surface cover). *Desmoschoenus, Austrofestuca* and *Euphorbia glauca* were probably common at foredune sites and backdune sites experiencing high rates of sedimentation. *Euphorbia glauca* was described by COCKAYNE (1909) as common and was still relatively abundant in the 1960s. *Pimelea lyallii* (Sand Daphne), *Coprosma acerosa* (Sand Coprosma), *Gentiana saxosa* and *Raoulia hookeri* were probably also widespread in relatively sheltered backdune and deflation areas. The long-walled parabolic dunes described above lay to landward of this foredune environment in 1958.

The extent and density of *Ammophila* increased between 1958 and 1978 (Figure 2). By 1978, *Ammophila* was present in dense patches up to 750 m inland. A continuous band of *Ammophila* occupied the former foredune environment. The width and density of this band decreased towards Duck Creek. A continuous, though topographically irregular foredune was present (Stage III after HESP, 1988). The extent and density of *Ammophila* in the study area continued to increase between 1978 and 1998. During this period *Ammophila* also spread from the 1960s plantings (east of the Homestead) about 700 m along the north-eastern margin of the dune system (Figure 2).

The proportion of the study area dominated by *Ammophila* increased from 1.4 ha in 1958 to 17.8 ha in 1978 to 74.9 ha in 1998. Therefore, the area dominated by *Ammophila* increased 5,204 per cent in the period 1958–1998. The area with little or no *Ammophila* (0–5 percent ground cover) declined 46 per cent over the same period.

Available aerial photographs show that *Ammophila* spread from the south in Mason Bay (taking approximately 25 years to form a continuous foredune between Martins Creek and Duck Creek). *Ammophila* invasion of the transgressive dune system in Masons Bay is continuing. In contrast, *Ammophila* became the dominant foredune and backdune species at the Doughboy Bay site over a much shorter period. The area of *Ammophila* increased rapidly between 1977 and 1999 as the barrier prograded by the formation of foredune ridges, from

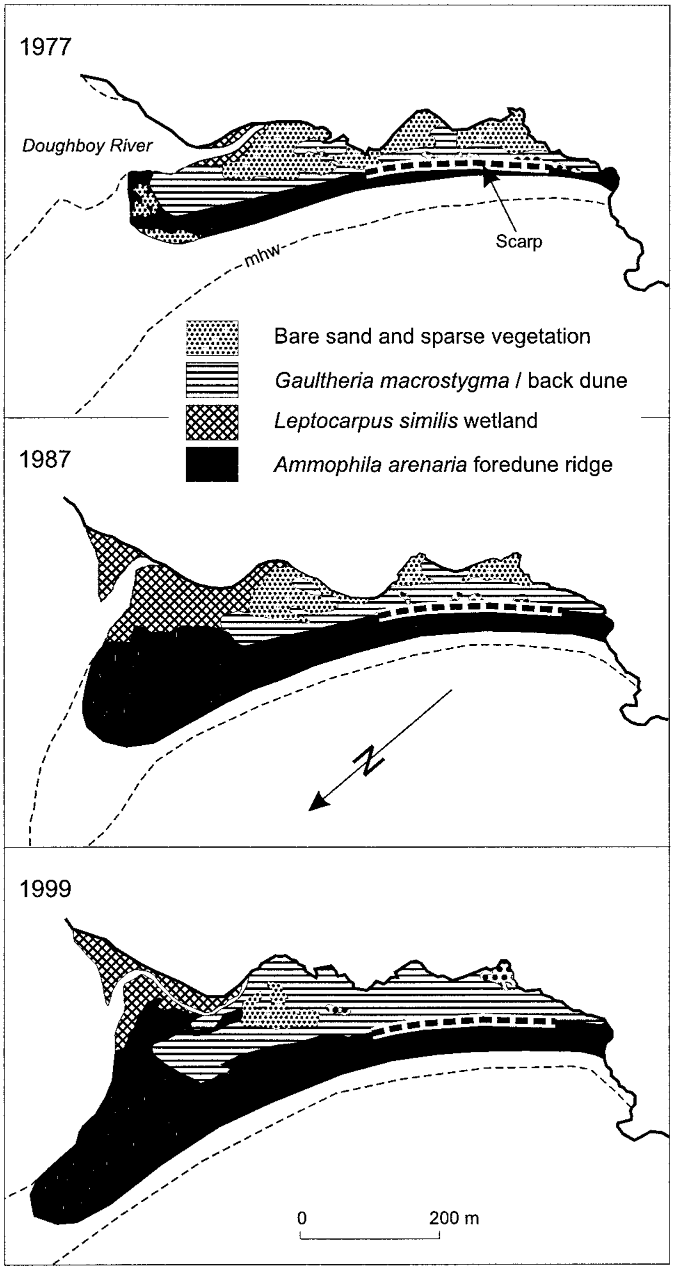

Figure 3. Morphology and plant cover of parabolic dune number six (in 1998). The contemporary dimensions of the foredune complex are compared with Cockayne's (1909) description of the foredune in 1908.

about 1.7 ha in 1977 to about 7.0 ha in 1999, a 412 per cent increase. At the same time the barrier prograded seawards (45–60 m) and towards the north (140 m) (Figure 3). The foredune ridges formed since 1977 have been colonised by *Ammophila* and now *Ammophila* is the only species inhabiting the stoss face of the modern foredune. There is no evidence, exposed rhizome for example, that *Desmoschoenus* has ever formed a significant cover on the foredune ridges, though a handful of isolated plants were observed in 1999.

Landform Development and Vegetation Change

Since the arrival of *Ammophila* the foredune in central Mason Bay study area has undergone considerable change. COCKAYNE (1909) described aspects of the pre-*Ammophila* dune landscape and dune flora of Mason Bay. In 1908 the foredune comprised a line of "low hummocks", 2–3 m high. The probable position and elevation of these dunes relative to the modern foredune complex is shown in Figure 4. COCKAYNE's description of the foredune is consistent with the dune landscape as can be discerned from the 1958 aerial photographs, soon after *Ammophila* established north of Martins Creek. The aerial photographs indicate a hummocky, discontinuous foredune, probably equivalent to the Stage IV foredune of HESP (1988).

The foredune complex developed between 1958 and 1978 as adjacent shadow dunes coalesced and *Ammophila* established a semi-uniform vegetation cover. The foredune is now a relatively massive landform termed a 'foredune complex' (after DOING, 1985). Deposition of sand across the Mason Bay foredune complex has continued as a result of: (1) formation of minor blowouts affecting the stoss face of the foredune; and (2) erosion and transport of sands across the beach during episodes of strong onshore winds. During the latter, sand is transported and deposited across the width of the foredune complex, well inland of the crest. Both processes appear to contribute to the vertical accretion and lateral growth of the foredune complex. Between 1978 and 1998 the morphology of the stoss face of the foredune complex has become more regular as the density of *Ammophila* increased and the extent and frequency of foredune blowouts declined. Narrow blowouts of a few metres wide and 20 m or so deep still occur, but these appear short-lived and are minor compared with the mass of the foredune complex. Periodic scarping during storm conditions limits the growth of *Ammophila* down the lower slopes of the stoss face of the foredune complex; hence, the plan configuration of the seaward edge of the foredune complex has become very regular since the establishment of *Ammophila* (Figure 2).

The long-walled parabolic dunes in the central Mason Bay study area developed before *Ammophila* invasion—they are present in the 1958 aerial photographs and were briefly described by COCKAYNE (1909). They are active transgressive dunes. Their depositional lobes have migrated at average rates of 5.0–7.5 m per year since 1978. The morphology and plant cover of parabolic dune number six is typical of these landforms. Four morphologic components are recognisable: (1) the deflation zone; (2) an area of active erosion incorporating the 'throat'; (3) a depositional lobe comprising a complex of coppice and shadow dunes; and (4) shared trailing arms (Figure 4). These elements of the parabolic dune have been maintained as the throat and depositional lobe advanced inland and the trailing arms lengthened in the period 1978 to 1998.

Live *Desmoschoenus* was observed during 1999 in the deflation zones of most of the parabolic dunes in the study area, (although most was moribund); on the level surfaces of the trailing arms (with *Ammophila* and a range of native dune and opportunistic species); and, occasionally, forming isolated

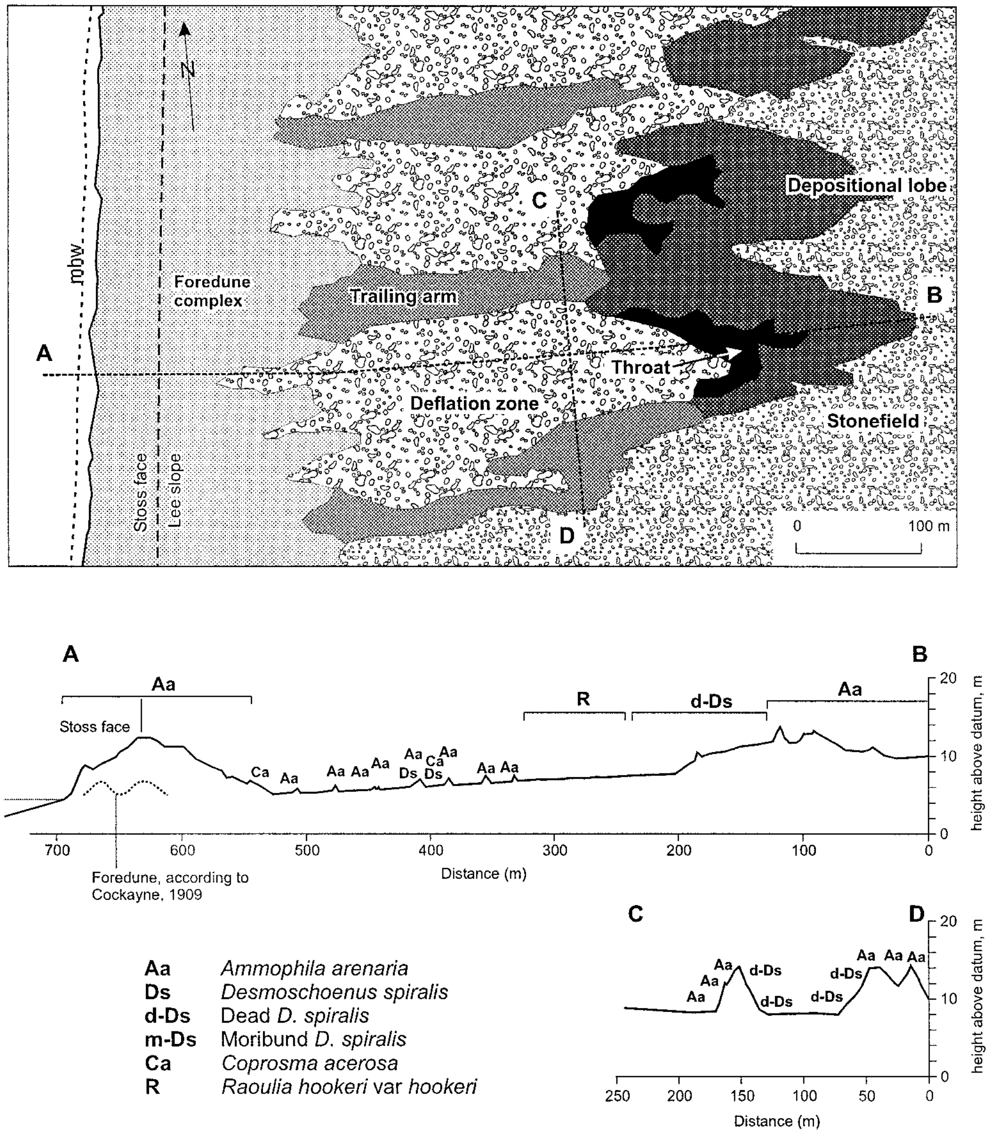

Figure 4. Plant species associated with the foredune complex (stoss and backdune slopes), trailing arms, deflation zones and depositional lobes. Values based on random survey of all long-walled parabolic dunes between Duck Creek and Martins Creek.

shadow dunes in the depositional lobes. Aerial photography (1958) and the widespread occurrence of dead root material in the eroding faces of the trailing arms and across the throat area shows that *Desmoschoenus* was, until recently, the dominant sand-binding species on these dunes. These dunes are now evolving in conjunction with *Ammophila,* which accounts for about half the plant cover across the trailing arms, less than half the total plant cover in the deflation zones and over 90 percent of the plant cover in the depositional lobes (Figure 5).

The pre-*Ammophila* barrier in Doughboy Bay probably comprised a relatively simple foredune complex, 100–150 m wide (Figure 6a). Some time in the mid 1900s (ca. 1960) an exceptional storm event eroded the front of the barrier. At this time both *Desmoschoenus* and *Ammophila* were probably present (Figure 6b), or *Ammophila* arrived soon after the storm. Subsequent, post-storm, progradation occurred in conjunction with *Ammophila,* not *Desmoschoenus* (Figure 6c & 6d) as successive foredune ridges established seawards of the former storm scarp. *Ammophila* now forms a dense cover across the stoss face of the contemporary foredune and a relatively sparse cover further inland. *Desmoschoenus* is absent from the foredune ridge section of the barrier. The storm scarp, therefore, separates the older *Desmoschoenus* barrier from the foredune ridge landscape associated with *Ammophila*. *Ammophila* and *Desmoschoenus* occur landward of the scarp, where *Gaultheria macrostigma* and other creeping species form a dense mat and where sand movement is nil. Neither species will survive if stability continues.

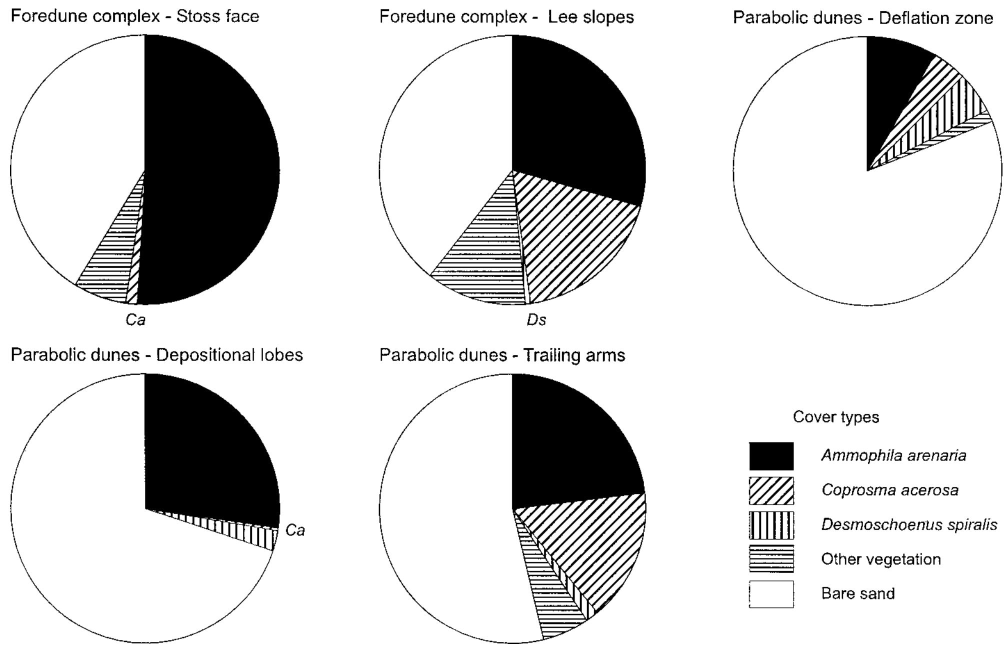

Figure 5. Recent progradational history of the southern dune system, Doughboy Bay, 1977–1999. Progradation has occurred in conjunction with *Ammophila arenaria. Desmoschoenus spiralis* is now restricted to the remnant barrier landward of the storm scarp.

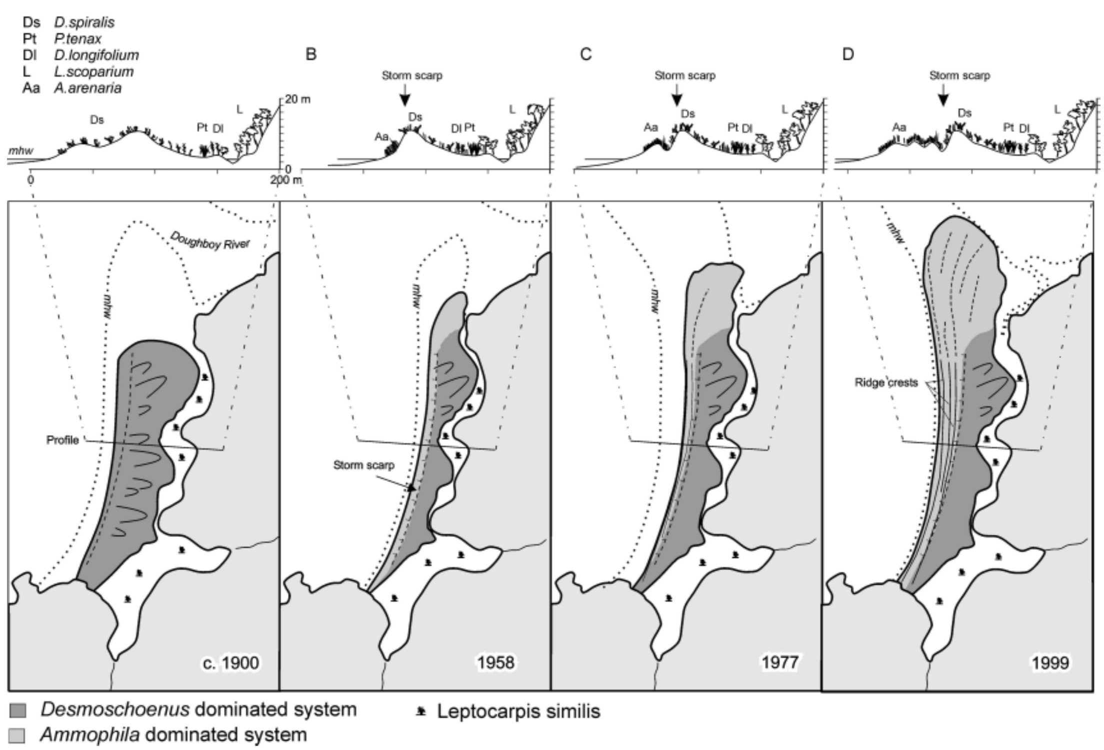

Figure 6. Interpretation of coastal change and *Ammophila* invasion, southern dune system, Doughboy Bay, *ca.* 1900–1999.

DISCUSSION

Ammophila Dispersal and Invasion

The establishment of *Ammophila* in the Mason Bay study area probably resulted from clonal spread, since reproduction by seed is thought to be exceptional (HUISKES, 1979). Fragments of rhizome are tolerant of seawater rafting for at least 8 tidal cycles (BAYE, 1990) and probably much longer (*e.g.* HEYLIGERS, 1985). Fragments of rhizome could have entered the sea in southern Mason Bay, during foredune scarping; and then been transported alongshore by nearshore currents and into the foredune environment by storm wave swash. This process may have occurred during a single storm event or phase of storminess, since most of the patches of *Ammophila* in 1958 in the study area appear of similar age (3–5 years).

Ammophila is most likely to have established in the interdune hollows of the study area, some distance inland of the mean high tide line, following deposition of rhizomes during storm conditions. Storm-wave deposition of rhizome propagules would have been assisted by the discontinuous foredune as it existed in 1958. The contemporary *Desmoschoenus* foredunes north of Duck Creek are typically low shadow dunes 2–4 m high, with multiple interdune openings at about the level of the spring high tide line. Interdune hollows in the foredune are flooded during storm events and commonly choked with flotsam and wind-blown material.

Successful *Ammophila* dispersal may rely on extreme storm events that are able to both erode propagules from the face of the foredune and deposit them in suitable locations. *Ammophila* is intolerant of substrate salt concentrations in excess of 1–1.5 percent (HUISKES, 1979; CHAPMAN, 1964) and may have difficulty establishing low on the stoss face of *Desmoschoenus* foredunes, in circumstances where inundation is common. *Ammophila* rhizomes blown or washed well inland, beyond the usual reach of storm waves, may stand the best chance of survival. Successful establishment of *Ammophila* may also depend on favourable meteorological conditions following transport and deposition of rhizomes. *Ammophila* establishment, therefore, may be episodic, even where the supply of rhizome material is constant.

Two other factors may have affected the potential for *Ammophila* to establish on or close to the stoss face of the former foredune in Mason Bay. Compared with coasts in southeast Australia, Europe and elsewhere, the study site lacks herbaceous pioneer annuals (the 'ephemerous tidemark' and 'perennial tidemark' communities of DOING (1985)). Species such as *Cakile maritime* may provide suitable conditions for *Ammophila* establishment across incipient foredunes but have only recently established in the study area. Secondly, berm development is unusual along Mason Bay beach and waves frequently cut the toe of the foredune.

Indigenous Species Displacement

Displacement of *Desmoschoenus* and *Austrofestuca* occurred rapidly following *Ammophila* invasion in central Mason Bay and Doughboy Bay. Between 1958 and 1978 *Ammophila* established a single, continuous foredune between Martin's Creek and Duck Creek. Over the same period, *Desmoschoenus* and *Austrofestuca* were displaced from the foredune and generally lost from the adjoining parabolic dunes. These processes of foredune development and indigenous foredune species displacement are ongoing north of Duck Creek. *Austrofestuca littoralis* and *Euphorbia glauca,* described by COCKAYNE as common in 1908, are now also absent from the foredune and parabolic dune environment in the Mason Bay study area.

Burial is probably the principle mechanism of indigenous species displacement. Individual *Ammophila* plants respond to burial by rapid production of elongated stem internodes (HUISKES, 1979). Shoots develop from these nodes, which then produce leaves upon reaching the surface. This process is repeated if sand supply continues, eventually producing a tussock habit (CHAPMAN, 1964). These tussocks create eddies or vortices in the lee of the plant during phases of onshore sand transport that tend to produce a pyramidal-shaped shadow dune (HESP, 1981). *Ammophila* shadow dune development results in areas of rapid accretion. As individual dunes develop intervening depressions may experience intense erosion. Sand deposited in the lee of these dunes, or as depositional lobes downwind of interdune deflation areas, may extend the influence of the first line of *Ammophila* shadow dunes well inland (Figure 7a). *Desmoschoenus* located in the lee of the initial *Ammophila* plant and in the new interdune hollows may experience lethal rates of accretion and erosion, respectively.

These processes may, over time, establish a massive foredune complex where none existed previously. Subsequent blowout development across the stoss face may contribute to the vertical accretion of the foredune complex (Figure 7b), which may also work to maintain *Ammophila* vigor. All plant species experience stress in the deflation areas of these blowouts, however, *Ammophila* plants on the margins of the deflation basin and across the depositional lobes experience renewed growth following accelerated sand deposition. Subsequent accretion and recolonisation by *Ammophila* may rapidly close the blowout.

Ammophila invasion and concomitant dune development in the Mason Bay study area appears to result in rates of sand accretion (and erosion) that exceed the tolerance of native dune species. *Ammophila* is known to accelerate rates of sand accretion (CHAPMAN, 1964) and burial is recognised as a strong selective force in dune ecology (MAUN, 1998). The ability of a plant to survive burial includes the plants tolerance of darkness and capacity to grow up through sand. *Ammophila* is able to tolerate rates of sand accumulation of up to 1 m per year (WILLIS *et al.,* 1959; RANWELL, 1972), although experimental work indicates instantaneous total burial will kill most specimens (SYKES and WILSON, 1990a). However, SYKES and WILSON (1990b) have demonstrated that *Ammophila* is much more tolerant of darkness (surviving burial for 117 days) than the native foredune species; *Austrofestuca* (37 days); *Euphorbia* (50 days); or *Desmoschoenus* (67 days). *Ammophila* may possess other competitive advantages (tolerance of drought, for example), but these are probably of minor importance compared to the ability of this species to initiate and survive rapid sand accumulation.

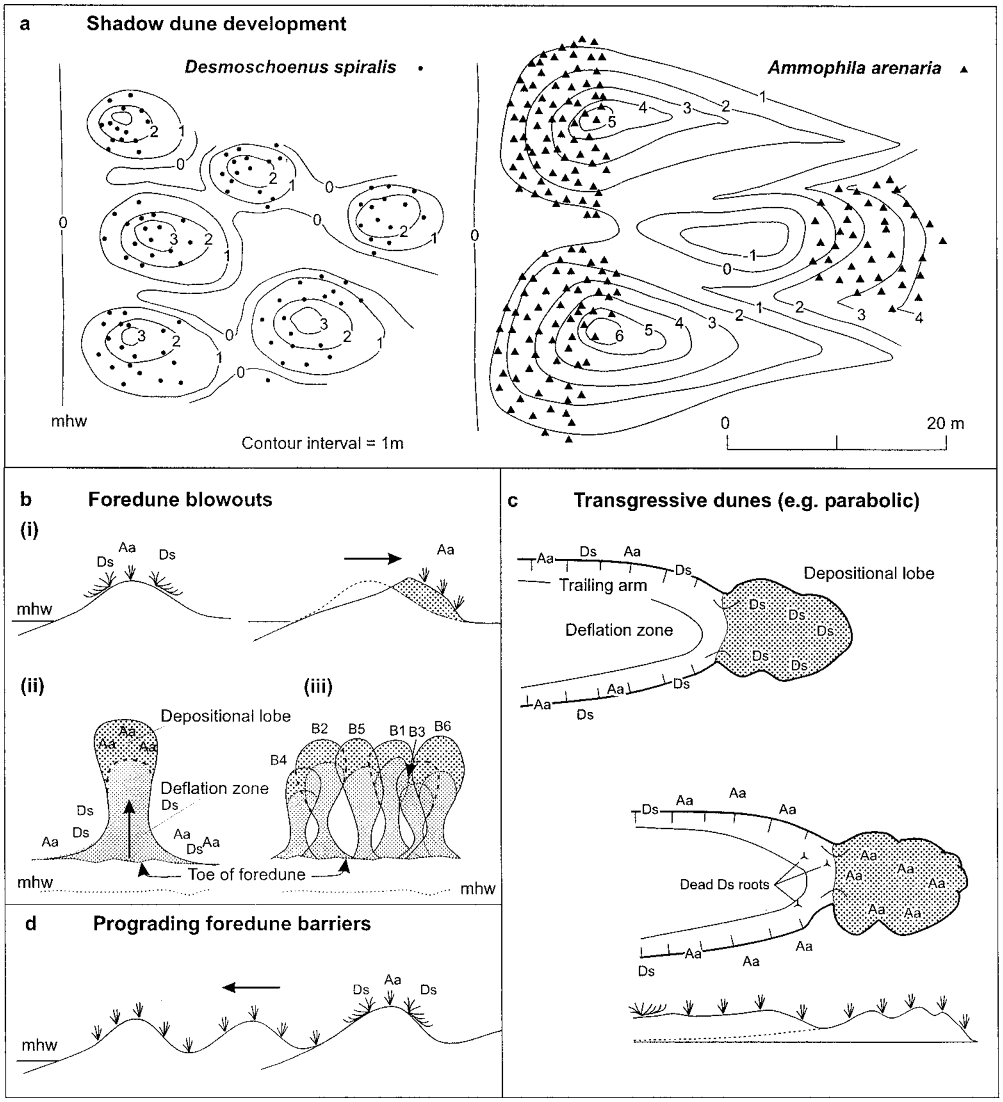

Figure 7. Interpretations of landform development and *Ammophila* invasion in the study areas.

Displacement of *Desmoschoenus* across the long-walled parabolic dunes in Mason Bay has also been rapid since the establishment of *Ammophila.* This process is an inevitable consequence of dune migration. The throat and depositional lobes are eroded as the dunes advance. The eroded sand is transported downwind and landward, usually through a narrow throat, or multiple throats, to contribute to the progressive construction of a new depositional lobe, progressively landward of the former (Figure 7c). In this fashion, the depositional lobes are being continually recycled. The destruction of *Desmoschoenus* is, therefore, a natural process. The failure of *Desmoschoenus* to re-establish in the depositional lobes and trailing arms is a consequence of competition with *Ammophila. Ammophila* appears better able and more aggressive at colonising the depositional lobes of these landforms. Once established, *Ammophila* may displace indigenous species by accelerating accretion beyond the survival threshold of these species. At the same time the indigenous species in the depositional lobe and throat zones are destroyed as the dune advances downwind. The trailing arms are relatively stable and hence retain higher indigenous species diversity. Secondly, where *Desmoschoenus* is able to establish in the depositional lobes, it is probably displaced by burial.

Finally, *Ammophila* invasion may be very rapid on coasts experiencing progradation (Figure 7d). Associated loss of native dune species may be equally rapid. *Ammophila* colonized developing foredunes at Doughboy Bay following a significant storm event more rapidly than *Desmoschoenus.* In this case *Ammophila* invasion and *Desmoschoenus* displacement may be very rapid, of the order of years. In such dynamic circumstances inter-specific competition for nutrients is unlikely to be a significant displacement mechanism.

CONCLUSIONS

In summary, *Ammophila* invasion and *Desmoschoenus* displacement in Mason Bay and at Doughboy Bay is associated with at least four processes of landform development (Figure 7): (a) shadow dune and foredune development; (b) blowout development; (c) parabolic dune migration; and (d) barrier progradation.

Ammophila invasion of the active dune systems examined is clearly associated with dune forming processes. Competition for nutrients is almost certainly important in semi-stable situations, but not in dynamic geomorphic situations. In such circumstances *Ammophila* traps sand and builds dune at rates that exceed the threshold of tolerance of all native species in the sites examined. The primary mechanism of native species displacement appears to be burial rather than competition for nutrients. At the sites examined *Desmoschoenus* displacement is most rapid in situations of active sedimentation and dune development.

There is no evidence that the relatively high tolerance of *Desmoschoenus* to salt will allow it to occupy the lower stoss face of the foredune as observed by PARTRIDGE (1995). *Desmoschoenus* cannot co-exist with *Ammophila* in the active dune systems of the study areas and is threatened with local extermination if *Ammophila* invasion continues.

EPILOGUE

The Department of Conservation commenced aerial herbicide eradication of *Ammophila* in Doughboy Bay in January 1999. *Ammophila* is to be eradicated from all three dune systems. This program was extended to include Mason Bay in January 2001. *Ammophila* has been virtually eradicated from the southern dune system in Doughboy Bay after three applications of herbicide (1999–2001). A new dune landscape is developing.

ACKNOWLEDGMENTS

The authors are grateful for the cooperation and support extended by the Department of Conservation, Southland Conservancy and Stewart Island Field Center over several years; particularly Chrissy Wickes; Mr Murray Nieuwenhuyse; and Dr Carol West. We would also like to thank Mr Bill Mooney (cartography) and Mr Bill Moffat (Southeast Air). Mike Hilton would like to gratefully acknowledge the hospitality of the Department of Geography and Environmental Studies at the University of Tasmania and Department of Geography and Environmental Studies at the University of Adelaide, while on sabbatical leave during 2001.

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