MARRAM GRASS (*AMMOPHILA ARENARIA*) AND COASTAL SAND STABILITY IN NEW ZEALAND

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ABSTRACT

The sand-binding plant *Ammophila arenaria* (L.) Link, commonly known as marram grass, has many characteristics which contribute to its usefulness in the initial stages of stabilisation of coastal sand and account for its selection for this purpose in most temperate countries. Research and experience in New Zealand have demonstrated the success of revegetation programmes based on its use in a planned vegetation succession, culminating in the permanent stabilisation of extensive sand drifts. Except on the seaward face of the current foredune, native sand-binding plants grow less vigorously than *A. arenaria*. For sites behind the foredune crest, use of *A. arenaria* offers the most reliable basis for prevention and arrest of sand mobility and the commencement of an effective vegetation succession involving native or exotic plants. Where rabbits have been eliminated from these sites and some degree of sand stability can be established and maintained, native sand dune species would be an appropriate choice for revegetation programmes. Use of *A. arenaria* as a temporary nurse for other dune species is currently under investigation.

Keywords: coastal sand; erosion; marram grass; revegetation; stabilisation; *Ammophila arenaria*.

INTRODUCTION

New Zealand’s coastal sand dunes cover a total of 305 000 ha, 80% of which are in the North Island (van Kraayenoord 1986). They form a strip 0.1–20 km wide which is subject to wind erosion wherever the sand is exposed and allowed to dry out. In pre-human times New Zealand vegetation was not subject to the clearing, burning, trampling, grazing, browsing, and other disturbance that commenced with Polynesian settlement between A.D. 1100 and 1300 and escalated with European colonisation. In the absence of human activity it is almost certain that areas behind the current foredune would have supported a vigorous and diverse flora that minimised exposure of sand during storm events and ensured rapid regrowth across any breach in the vegetation cover. Human influence brought about the destruction and reduced effectiveness of many indigenous species. Greater areas of sand were uncovered and exposed to wind action, with the consequence that massive mobile dunes became a common coastal feature. The destructiveness of these dunes was all too apparent by the end of the nineteenth century and the New Zealand Government was eventually called to attend to the problem (Gadgil & Ede 1998). Stabilisation of 115 000 ha of drifting sand was accomplished by revegetation, using a method of successional planting recommended by Cockayne (1911). This involved firstly the planting of *A. arenaria* to arrest major surface sand movement; secondly, the sowing of seed of *Lupinus arboreus* Sims (tree lupin), a nitrogen-fixing shrub which completed the initial ground coverage; and finally, the planting of *Pinus radiata* D. Don trees which provided permanent cover and the required degree of sand stability. The resulting forests have continued to fulfil their protective role, which is not compromised by management for sustained timber production (Wendelken 1974).

Salt-laden winds, characteristic of the coastal environment, are particularly frequent and strong in New Zealand latitudes (34°– 48°S) and cause both erosion and accretion of surface sand, with accompanying sand-blasting effects. Mobile sand consists mainly of single grains of rock and shell. It contains little or no organic material and therefore has no additional moisture-retaining properties, no source of plant-available nitrogen compounds, and only a sparse microbial population (Hassouna & Wareing 1964).

Very few plant species are able to tolerate the combination of edaphic and climatic conditions that exists on the dunes until some degree of stability, shelter, and a rudimentary organic matter cycling mechanism have been established. Plants that colonise unstable sand have become adapted to this habitat through the development of specialised anatomical and physiological characteristics. They exert an incremental effect on the ecosystem by trapping sand; by creating a microclimate at the ground surface which reduces direct insolation and moisture loss; and by developing a network of underground roots and rhizomes which hold and bind the sand. Each of these processes modifies the environment, increasing its suitability as a habitat for less-specialised plants and other organisms which may eventually replace the initial colonisers. As conditions become favourable to a wider range of species, the succession will continue until a recognisable association is formed.

Cockayne (1911) described *Spinifex hirsutus* (now *Spinifex sericeus* R. Br.), *Scirpus frondosus* (now *Desmoschoenus spiralis* (A. Rich.) Hook. F.), and *Euphorbia glauca* Forst.f. as specialised native New Zealand sand-binding species which play a major role in the colonisation of wind-blown sand and thus initiate the sand stabilisation process. His choice of *A. arenaria* as the recommended initial sand-binding component in an artificial revegetation succession was influenced by the urgency of need for a species with known and tested characteristics. One hundred years of research on sand stabilisation in Europe, and other more recent work in the United States, South Africa, and Australasia had already shown *A. arenaria* to be the most effective sand-binding species (Cockayne 1911). Because it was already present in New Zealand, known to grow vigorously under local conditions, and to be relatively inexpensive to establish on a large scale, research into the suitability of other species was difficult to justify. In practice, the planting procedure was successful and continued to be recommended and used for more than 70 years. The nationwide effectiveness of the *A. arenaria* / *L. arboreus* / *P. radiata* succession can be attributed to the sound ecological principles on which it was based.

During the last 20 years, two events have forced the consideration of species other than *A. arenaria, L. arboreus,* and *P. radiata* for use in current sand stabilisation projects. One was the onset of lupin blight, a disease caused by the fungus *Colletotrichum gloeosporioides*

(Penzig) Penzig & Saccardo, which virtually removed lupin from the dunes (Dick 1994). The other was the passing of the 1991 Resource Management Act which sanctioned a widespread desire for land managers to preserve and restore the "natural character" of the resources under their care. This legislation accorded well with the aims of a growing conservation/ preservation movement and was interpreted by many resource management agencies as a directive for replacement of exotic plants with native species wherever possible.

The urgency for preventing and arresting sand drift inland from the coastal strip is as great as ever. In sand stabilisation work, where the time factor is often crucial and setbacks can exacerbate the original erosion problem, it is essential that the consequences of changes to well-tried methods should be understood before they are attempted. The purpose of this study was to bring together information relating to *A. arenaria* which may have a bearing on its relative usefulness wherever the presence of unstable or drifting sand is considered to be undesirable. Practical experience over a long period of time has proved the value of the species in this context. Close examination of its attributes will be needed as part of any meaningful comparison with species proposed as alternatives.

DISTRIBUTION

Ammophila arenaria (Syn. *A. arundinacea; Calamagrostis arenaria; Psamma arenaria*) has been described as the world's best known and most widespread sand plant (Esler 1970). It has been present in New Zealand for at least 125 years. It was probably introduced from Australia for the purpose of sand stabilisation in the Wellington area (Crawford 1874). *Ammophila arenaria* is native to western Europe, where it is abundant and often dominant on mobile and semi-fixed dunes of all except Arctic coasts (Huiskes 1979). A naturally occurring sterile intergeneric hybrid, *Ammocalamagrostis baltica* (Fl.) P. Fourn., the product of the crossing of *Ammophila arenaria* and *Calamagrostis epigejos* (L.) Roth, is locally abundant in three isolated British coastal areas, and in western Europe from Scandinavia to France (Hubbard 1954). Cockayne (1911) reported that *A. arenaria* had been introduced into North America, Australia, and North and South Africa, and it is now naturalised in most temperate coastal regions. In Australia it is present in all states except the Northern Territory (Harden 1993) and Queensland (Jessop & Toelken 1986). The latitudinal range appears to be approximately 30° to 63° in the Northern Hemisphere (Breckon & Barbour 1974; Huiskes 1979) and 30° to 48° in the Southern Hemisphere (Avis 1989; Harden 1993; Edgar & Connor 2000).

In New Zealand, *A. arenaria* has been planted on a large scale and has spread vegetatively and occasionally by seeding (Edgar & Connor 2000). It now dominates plant communities growing on partially stabilised sand in many parts of the country with the exception of the west coast of the South Island south of the Waiho River (Wardle 1991). In South Westland and Stewart Island it exists as isolated stands in otherwise native plant communities. *Ammophila arenaria* has been planted on inland sand dunes near Cromwell, in Erewhon Park in the Rangitata Valley, and on drifting pumice along the Desert Road north of Waiouru (van Kraayenoord 1986; Edgar & Connor 2000).

PLANT DESCRIPTION

Edgar & Connor (2000) described *Ammophila arenaria* as an erect perennial grass which forms compact tussocks up to 170 cm tall. It spreads horizontally and vertically through loose sand by means of woody underground rhizomes. These produce roots, erect shoots and branches at the nodes, and may be several metres long. The number of shoots (tillers) arising from the rhizomes is greater per unit area in unstable sand than in semi-fixed or fixed sand (Huiskes 1979). The dense, fibrous root system descends to 1–2 m (Wardle 1991).

Leaves are bluish-green, with smooth, overlapping sheaths. The blades are up to 6 mm wide, sharply pointed, rigid, and in-rolled, especially under dry conditions. They are closely ribbed and densely covered with minute hairs on the upper (inner) surface but smooth on the lower (outer) surface (Purer 1942). Flower heads or panicles develop in December and January as whitish, compact, narrow, cylindrical plumes which taper upwards. Although it is generally acknowledged that little seed is set under New Zealand conditions (Wardle 1991), Esler (1969) described abundant seedling development on dune flanks and the slip faces of dunes advancing across wet flats in the Manawatu region.

Adaptation to the Coastal Habitat

Tolerance to salinity and alkalinity

Although unable to survive direct contact with sea water (Fenton 1949) or concentrations of sodium chloride in the substrate exceeding 1.0% (Huiskes 1979), mature plants of *A. arenaria* can tolerate salt spray (Sykes & Wilson 1988). They successfully colonise the upper seaward slope and crest of the current foredune and sandy areas further inland (Wardle 1991). Sykes & Wilson (1988) found that the growth rate of *A. arenaria* seedlings was decreased by salt spray.

Vigorous colonies of *A. arenaria* have been found growing on sand with a pH value of 9.06 (Willis *et al.* 1959a), but the species does not occur where pH is lower than 4.5 (Lux 1966).

Tolerance to wind action

Most plant species are unable to tolerate the effects of wind force and associated dry sand movement that characterise the open dune environment and result in physical battering, abrasion, and desiccation. *Ammophila arenaria*, with its tough wiry leaves, extensive rhizomes, and dense deep root system, is well adapted to this environment. Smooth outer leaf surfaces and pointed leaf shape offer minimum resistance to wind and resist abrasion. Concentration of stomata on the upper (inner) ribbed and hairy surface of the leaves, which become more tightly inrolled under dry conditions, minimises their exposure to air movement. This reduces the transpiration rate, which would otherwise be high under the influence of desiccating winds (Purer 1942; Pavlik 1985). Growing points of shoots are located underground where they are protected from adverse conditions other than extremes of drought or sand erosion.

Tolerance to sand movement (accretion and erosion)

Sand grains are held together by the underground network of deep fibrous *A. arenaria* roots and extensive woody rhizomes. This network develops rapidly under favourable conditions. In normal reclamation work in New Zealand, planting at 1.2 m spacing with routine application of nitrogenous fertiliser (Wendelken 1974) was found to stabilise sand sufficiently for introduction of secondary successional species after 1 year. This implies expectation of a horizontal underground extension rate of at least 0.6 m/yr. Below-ground dry matter accumulation of 2–4 t/ha (to a depth of 1 m) has been recorded at this stage (Gadgil 1971).

Ammophila arenaria is an efficient sand collector as well as a sand binder (Cockayne 1911; Hesp 2000). The upright tillers arrest wind-blown sand grains which fall and contribute to the formation of sand mounds around the base of the tussocks. A plant growing in loose sand will have a number of tillers radiating from the tips of vertical rhizomes at a point near the sand surface. If the plant becomes more deeply buried, further rhizomes will form and produce tillers near the new sand surface (Cockayne 1911). Initiation of new roots tends to be localised near the sand surface and is especially frequent in freshly-buried shoot bases (Willis 1965). *Ammophila arenaria* plants have been known to survive sand burial rates of 80–100 cm/yr (Huiskes 1979). This faculty is thought to be linked with ability to tolerate relatively long periods of total darkness (Sykes & Wilson 1990).

Maintenance of a net increase in biomass seems to be dependent on sand accretion rates of up to 40 cm/yr (Marshall 1965). Although gradual loss of vigour associated with increase in sand stability has received comment since the mid 1800s, the reasons remain obscure. Theories put forward include inability to tolerate a changed microenvironment, inefficiency in replacement of tissues which have a shorter lifespan than the plant as a whole, and physiological senescence. Van der Putten & Troelstra (1990) rejected suggestions that changes in soil fertility, loss of calcium carbonate, accumulation of organic matter, reduced salt spray, or increased plant competition could account for the decline on the grounds of the relatively long time period required for their influence to take effect. They produced evidence suggesting that penetration of newly-deposited sand reduces exposure to harmful soil organisms which colonise older soil. More recently, combinations of fungi and nematodes, rather than single species, were found to be associated with the decline on coastal foredunes in the Netherlands (de Rooij-van der Goes 1995). Willis (1965) observed an increase in vigour when nutrients (particularly nitrogen) were applied. The magnitude of this increase was greater under conditions of active sand accretion, indicating that nutrient addition did not compensate for the effect of fresh sand. Wallén (1980) found that the lifespan of above-ground biomass increases with time. He maintained that the decline in net biomass production does not correspond to a decline in gross production, but represents a change in the ratio of assimilating to non-assimilating tissue. This ratio change progresses towards a steady state in which annual respiration equals annual assimilation and there is no further net increase in biomass.

Tolerance to temperature dynamics and drought

Regular wind action promotes high rates of moisture loss from any material characterised by a single-grain structure and low water-storage capacity. Absence of shade means that summer air temperatures on unvegetated sand dunes are relatively high, with wide daily and hourly fluctuations. Few measurements of the physical factors affecting plant growth on coastal dunes have been reported in New Zealand. Cockayne (1911) recorded a temperature of 52°C in surface sand at Levin in summer. In black ironsand near Wanganui the temperature at a depth of 7.5 cm was 33°C when air temperature was only 19°C. At a comparable latitude in North Carolina, Oosting & Billings (1942) recorded maximum temperatures of 52°, 35°, and 32°C at sand depths of 0, 10, and 25 cm. They noted that major changes in air temperature influenced readings at 10 cm depth, and that on sunny days surface temperatures exceeded those at 10 cm by 5°–20°C. Willis *et al*. (1959b) recorded a summer diurnal fluctuation of 10°–35°C near the surface of sand dunes in southern England.

High temperatures and constant exposure to wind (gales of the order of 80 km/h occur frequently in New Zealand) increase both evapotranspiration and the tendency for surface sand layers to dry out. Such conditions do not inhibit survival of *A. arenaria*, although growth is probably confined to periods when they are less extreme. Plants are known to survive fire; in fact, burning soon after planting was once a method used in the Hebrides to reduce wind damage (Hobbs *et al*. 1983). Huiskes (1979) observed that growth of well-watered *A. arenaria* plants in the glasshouse during summer was not affected by temperatures exceeding 50°C. Although older plants are strongly drought tolerant, seedlings are vulnerable to desiccation and survive to maturity only in sites such as dune slacks that remain damp for considerable periods of time (Huiskes 1979). Waterlogging reduces growth rates (Carey & Oliver 1918).

Tolerance to low nutrient status of sand

Plant nutrients contained in recently deposited coastal sand are unlikely to be available in the proportions or amounts required for healthy growth of most species. In this free-draining medium, soluble compounds released during weathering of component minerals are subject to rapid leaching from the rooting zone. Sea spray, rainfall, and incoming sand are the only natural external sources of plant nutrients. The negligible organic matter content means that supplies of nitrogen, a major plant nutrient element, are inherently low and inadequate for growth of many species. Very low total nitrogen levels (<0.01%) are characteristic of mobile dune sand (Willis *et al*. 1959a; Gadgil 1971; Barr & McKenzie 1976; Kachi & Hirose 1983; Hawke & Maun 1988; Van der Putten & Troelstra 1990); deficiencies of other nutrient elements occur less frequently and depend mainly on mineral composition, which varies with geographical location. Distance from the shore will determine inputs from sea spray; rainfall may contribute nutrients but will also promote leaching.

Ability to colonise unstable sand implies both tolerance of nutrient imbalance and efficient use of any nitrogen that becomes available. The success of *A. arenaria* on sand dunes in most temperate regions is evidence of this ability. Willis (1965) showed that although *A. arenaria* could grow in unstable sand of low nutrient status, shoot numbers, height, and dry weight were increased by addition of phosphorus, potassium, and nitrogen. The response to nitrogen was particularly marked. No other nutrient deficiency symptoms have been reported for this species.

In sand containing negligible amounts of nitrogen, luxuriant stands of *A. arenaria* have been shown to support populations of free-living nitrogen-fixing bacteria such as *Azotobacter* in the vicinity of the roots (Hassouna & Wareing 1964; Abdel Wahab & Wareing 1980). The activity of these organisms appears to play an important part in the nitrogen nutrition of *A. arenaria*.

Leclerc & Robin (1983) found that the nitrogen metabolism of *A. arenaria* plants is sensitive to change in soil water potential and nitrate content. When soil moisture levels are low (<2%), nitrogen assimilation rates decrease and nitrate is stored in the tissues. As soil moisture increases, nitrate reductase activity also increases, and the stored nitrate is consumed.

A study of the relationship between *A. arenaria*, the leguminous species *Lupinus arboreus*, and *Pinus radiata* led Mead & Gadgil (1978) to suggest that the speed of permanent cover development in the artificial sand dune vegetation succession may be controlled by the avidity of *A. arenaria* for fixed nitrogen. Efficient utilisation of fixed nitrogen derived from the lupins and the later release of this nitrogen (a consequence of suppression of *A. arenaria* by the trees and subsequent decomposition) appear to be important process components in the early stages of nitrogen cycling in the developing ecosystem. Above-ground nitrogen content of 7-year-old *A. arenaria* was doubled by the presence of *L. arboreus* but there was little increase in dry matter production (Gadgil 1976). Plant death and decomposition after tree canopy closure would have released this nitrogen at a time when tree roots were exploiting a large proportion of the soil volume and tree nitrogen requirements were greatest (Mead & Gadgil 1978).

Vesicular-arbuscular mycorrhizal fungi (probably *Endogone* spp.) have been observed in the roots of *A. arenaria* growing on semi-stabilised dunes but are rare in plants colonising mobile sand (Nicolson 1960). The fungus is thought to enhance plant nutrition by increasing the availability of less-soluble compounds in the sand.

Palatability

In New Zealand, sand dunes and their vegetation commonly support populations of rabbits, hares, and small rodents. Coastal dunes are sometimes accessible to feral goats (Walls 1998), deer (McKelvey 1999), and wild horses (Sale 1985). Throughout the country, farm managers often use sand dunes as extensive grazing areas for cattle, sheep, horses, and goats. Browsing animals are, therefore, a common component of the sand dune environment, and have a profound effect on the continuity and nature of the vegetation cover.

Although *A. arenaria* seedlings are eaten by rabbits (Esler 1969), mature plants are less vulnerable to browsing by rabbits and grazing stock. Cattle, sheep, and horses will eat *A. arenaria* only when other fodder is unavailable (Cockayne 1911). Colonies spread mainly by vegetative reproduction, and tiller replacement from underground stems usually compensates for browsing damage. Many other sand dune species are more dependent on seedling establishment for successful colonisation and these will be more vulnerable to the effects of browsing pressure. Esler (1969) described *S. sericeus* as the most palatable plant on the foredune of the Manawatu coast, implying that *A. arenaria* and *D. spiralis* were less severely affected by grazing and browsing animals.

Disease

Ammophila arenaria in New Zealand is free from major diseases (van Kraayenoord 1986). Three phytopathogenic fungi occurring on *A. arenaria*, but not considered to be important, are ergot (*Claviceps purpurea* (Fries) Tulasne), recorded on 12 native and 20 introduced grass species and widespread throughout New Zealand (Dingley 1969); *Uredo* sp., a rust associated with *A. arenaria* throughout New Zealand (McKenzie & Johnston 1999); and a leaf spot (*Colletotrichum graminicola* (Ces.) Wilson), recorded on *A. arenaria* on the Coromandel Peninsula and on Great Barrier Island and known to be common on other grasses (McKenzie & Latch 1984).

In the Netherlands, Van der Putten & Troelstra (1990) noted that organisms commonly found in soil (possibly nematodes and fungi — Van der Putten *et al.* 1990) can be harmful to *A. arenaria* and may be responsible for the decline in vigour which is associated with older communities on stabilised sand.

Sand-stabilising Potential

Stabilisation of coastal sand can be defined as the sum of processes which change potentially mobile sand into a permanently fixed substrate. These processes can be divided into those involving sand trapping and those involving sand binding (Cockayne 1911).

Because of their density and erect form, *A. arenaria* tussocks act as effective traps for wind-blown sand. Fallen grains accumulate into mounds at the base of the plants and tillers developing from the rhizomes grow upwards to the new surface (Cockayne 1911; Hesp 1979). Rapid formation of the deep root system and radial extension of rhizomes and roots contribute to the formation of a three-dimensional underground network which binds the grains together and holds the sand firmly. It is the capacity for both sand-collecting and sand-binding, together with a rapid growth rate in most temperate latitudes, that makes this species physically effective during the initial stages of sand stabilisation. On the Pacific coast of North America, Breckon & Barbour (1974) have noted foredune development associated with the spread of *A. arenaria* in areas where beach elevation was previously uniform. In describing sand dune vegetation of the Manawatu region of New Zealand, Esler (1970) pointed out that although *S. sericeus* is more effective than *A. arenaria* in stabilising the current foredune, the fixing of the extensive rear dune system has been largely dependent on the introduction of *A. arenaria* because there is no species among the native flora which is ecologically equivalent as a lee dune stabiliser.

One disadvantage of the tussock habit in sand reclamation work is that wind funnelling between widely spaced plants may cause erosion of sand which has not yet been penetrated by roots and rhizomes. High local windspeeds may be sufficient to excavate and dislodge individual plants and initiate blowout development. Remaining plants and the sand held by their roots then contribute to a “turret” topography (Esler 1970) which is typical of neglected plantings on exposed sites. The solution is the erection of physical barriers to arrest wind-blown sand and restore an even topography (Restall 1964). Replanting of *A. arenaria* is likely to be successful if adequate attention is paid to planting density, orientation of rows to present maximum plant resistance to prevailing winds, treatment with nitrogenous fertiliser, and restriction of animal and human access.

Interaction with Other Plant Species

Concern has been expressed that *A. arenaria*, introduced for sand stabilisation purposes, has displaced native plant species and altered the character of local sand dune communities in New Zealand (Norton 1991), Australia (Kirkpatrick & Harris 1995), and the United States (Breckon & Barbour 1974). In South Africa, a 1974 decision to phase out use of alien species for sand dune stabilisation allowed an exception in the case of *A. arenaria* (Avis 1989). This species was not regarded as invasive in the Cape Province and was considered to be more effective than any of the native plants in the creation of sand-arresting barriers. In New Zealand, several authors have commented on the invasiveness of *A. arenaria* and its current dominance at the expense of native species, especially *D. spiralis* (e.g., Smith *et al.* 1985; Johnson 1992; Wardle 1991; Partridge 1992, 1995).

At a site behind the current foredune in Hawke's Bay, Walls' (1998) evidence that *A. arenaria* was "squeezing out native plants" was unconvincing since total recorded vegetation cover did not exceed 40% even where rabbits and larger animals had been excluded for 8 years. The observed decline of *S. sericeus* after 6 years was probably due to the fact that this species was near to its landward limit (described by Esler (1970) as "a few chains from the beach"). At this stage *A. arenaria* occupied only 10-16% of the available area, and cover of *D. spiralis* remained at about 1%. Results from unreplicated exclosures indicated that browsing by animals, particularly rabbits, had an inhibitory effect on the rate of spread of *A. arenaria*, *Carex pumila* Thunb., *Coprosma acerosa* A. Cunn., and *S. sericeus.*

Esler (1970) described the "rising ascendancy" of *S. sericeus* over *A. arenaria* and *D. spiralis* on the current foredune of the Manawatu coastline. From a Southland study, Smith *et al.* (1985) concluded that *D. spiralis* had been displaced by *A. arenaria* on mobile sand at the top of the beach. Here *A. arenaria* was currently the major coloniser, stabilising the substrate and facilitating the establishment of prostrate species. A mixture of herbs, grasses, shrubs, and woody species including *Lagenophora pumila* (Forst. F.) Cheesm., *Phormium tenax* J.R. et G.Forst., and *Metrosideros umbellata* Cav. eventually replaced *A. arenaria* on stabilised sites where there was no further sand supply. In Otago and Southland, *Euphorbia glauca* has been found to co-exist with *A. arenaria* (Johnson 1992).

Research on inter-species relationships in *Pinus radiata* forest, planted to complete the stabilisation of drifting sand, showed that, although *A. arenaria* does not survive complete canopy closure by an overstorey, it can account for one-third (18–24 t/ha) of the total above-ground biomass in 4- to 5-year-old tree stands (Gadgil 1971, 1976).

Control Measures

Partridge (1995) showed conclusively that hand-pulling did not remove *A. arenaria* unless carried out frequently and over a long period. Rhizome material left in the ground actually grew more vigorously after hand-pulling, probably because sand was disturbed and older material was removed.

Selective herbicides have been used by the Department of Conservation to control the growth of *A. arenaria* in Southland, where its spread is considered to threaten the development of native species (Bergin 2000). The possibility that restriction or removal of *A. arenaria* may compromise sand stability has to be considered before any control or eradication measures are initiated. Spraying with the grass-specific herbicide Gallant (15 ml/litre) will kill above-ground *A. arenaria* material, but monitoring and follow-up treatment are necessary to ensure that regrowth from underground rhizomes is also killed. Gallant does not affect *D. spiralis*, which is a sedge, but other grasses should be protected from contact with the herbicide spray (Bergin 2000).

Planting Methods

Details of methods used for *A. arenaria* establishment in successful sand stabilisation projects in New Zealand have been described by Harrison-Smith (1939), Restall (1964), Wendelken (1974), and McKelvey (1999). Planting material is taken from a "nursery" area treated with a heavy dressing of nitrogenous fertiliser 2 years before winter lifting. Roots of well-developed tussocks are cut well below sand level with a sharp spade. Tillers with roots and rhizome buds attached are bundled in groups of approximately 500, top-trimmed to a length of 60 cm to reduce transpiration and stored so that roots are covered with damp sand. Handfuls of about 12 tillers are planted to a depth of about 40 cm at 1.2 m spacing. Prompt replacement of buried or blown-out plants is essential. All planting prescriptions involve the use of nitrogenous fertiliser at time of planting, and further applications at regular intervals are recommended (Wendelken 1974) for maintenance of vigour until organic matter cycling within the ecosystem becomes self-sustaining.

Hobbs *et al*. (1983) found that in the absence of active sand accretion, development of *A. arenaria* cover was more rapid when rhizomes were planted horizontally. Vertical rhizome placement was more successful if plants were subject to burial (20–30 cm of sand in the first year). Shoot production was closely related to the number of nodes and buds present on the transplant material. Placement of the rhizome growing point at a depth greater than 20 cm sometimes resulted in failure of shoots to reach the sand surface. Total defoliation at time of transplanting impeded new growth.

COMPARATIVE STUDIES

Consideration of the relative usefulness of any plant species is greatly facilitated by comparative studies carried out under identical conditions. Although Esler (1970) considered that *A. arenaria* has no equal as a sub-surface sand-binder, his observations of three sand-binding species on the Manawatu dunes led him to regard a dense tussock habit as a mixed blessing. Tussocks are very efficient sand traps, but when widely-spaced they tend to increase wind-channelling, erosion of unconsolidated sand between plants, and blowout development. Isolated plants of *A. arenaria* and *D. spiralis* frequently contribute to, and are destroyed by sand deflation in this way (Harrison-Smith 1939; Esler 1970). Esler pointed out that the fast-growing and prostrate surface rhizomes of *S. sericeus* trap sand grains more evenly across the sand surface, thus providing greater opportunity for the spread of underground plant parts into fresh sand deposits. Observations in the Manawatu (Esler 1978) showed that dunes formed under *A. arenaria* were steeper (24°– 28°) and higher (≥ 8 m) than those associated with *S. sericeus* (14°–16°; 6 m) and *D. spiralis* (8°–14°; < 3 m). This was attributed to the fact that above-ground shoot systems of both *S. sericeus* and *D. spiralis* are more extensive and diffuse than those of *A. arenaria*. In a study of the aerodynamic effects of vegetation on the Kaitorete Spit, Canterbury, Holland (1981) found that, individually, the dense erect tussocks of *A. arenaria* had a greater sand-trapping effect than the more diffuse tufts of *D. spiralis*. The decrease in windspeed to leeward of an *A. arenaria* tussock was more pronounced, while lateral windspeeds were greater, and this resulted in strong eddy formation. Lower leeward and lateral windspeeds associated with *D. spiralis* plants resulted in weaker eddying and deposition of smaller amounts of sand in mounds with a smoother topography. In spite of marked differences at the individual plant level, Holland could find no clear differences between the species in terms of interaction with sand movement at the community level.

Although *D. spiralis* is an efficient sand collector, it is a less effective sand-binder than either *A. arenaria* or *S. sericeus* because it grows more slowly (Holland 1981) and is less tolerant of erosion of sand around roots and buried rhizomes (Esler 1970). Holland (1981) observed that *D. spiralis* is less tolerant of exposed sites than *A. arenaria*, and that its rhizomes tend to develop more rapidly in a downslope direction than those of *A. arenaria*.

Partridge (1995) has shown that there are circumstances under which *A. arenaria* does not constitute a threat to *D. spiralis*. These include any situation in which marram growth is restricted by lower salt tolerance or an inadequate supply of fresh sand. Where moisture is not a growth-limiting factor, the two species can co-exist as a mixture even though *A. arenaria* may assume dominance.

DISCUSSION AND CONCLUSIONS

In terms of stabilisation of wind-blown sand, the effectiveness of vegetation cover will be determined by plant morphology, plant vigour, and the density, longevity, and extent of the plant community. These factors are all likely to be modified by wind energy, sand supply, and moisture availability. Since the beginning of the twentieth century it has been recognised that forest is the most effective cover for coastal sand (Cockayne 1911) because it is characterised by closely spaced, deep-rooted, long-lived plants with strong structural components. Trees do not establish readily in mobile sand under coastal conditions, and forests can develop only where some vegetation cover already exists and provides adequate shelter, shade, and organic matter. The intermediate but less permanent vegetation will in turn develop only where sand movement, wherever it occurs, has been partially arrested by sand-binding plants. Maximum sand stability can be achieved only where conditions favourable to forest development have been provided, either naturally or as a result of successional planting programmes. Inadequate shelter, shade, and organic matter will halt the vegetation succession at a stage where only the more tolerant herbaceous or shrubby plants persist. In this case the vegetation cover will be more vulnerable to disturbance and the protection afforded to the sand will be less permanent than that provided by forest. Conditions associated with the coastal strip located immediately behind the current foredune and extending inland for a variable distance are unlikely to be tolerated by forest trees. In this zone woody shrubs will represent the climax of the vegetation succession. They will form an effective plant cover only as long as they remain vigorous and undisturbed.

Current interest in restoration of the natural character of coastal sand dunes has stimulated a surge of interest in preservation of native plant species which are especially adapted to this environment. Debate continues about the methods that should be employed for their reintroduction. Due to human and animal interference, natural events, and regional climatic influences, most coastal dunes in New Zealand are now devoid of the native forest which would have been the most effective natural stabilising influence. Attempts to re-establish a native species succession should be encouraged wherever this is considered to be appropriate. On the other hand, it is important to realise that any activity resulting in wind erosion of dry sand, even on a small scale, should be avoided. Such activities include the choice of inappropriate species, since this can lead to planting failure and the escalation of blowouts. Bergin & Kimberley (1999) have pointed out that decisions to reconstruct native plant communities or to enrich remnant natural dune plant associations require justification from practical, as well as cultural, historical, and aesthetic viewpoints. This observation supports Cockayne's (1911) view that, while the general geological and botanical principles on which sand stabilisation techniques are based should never be violated, sound judgment founded on experience of local conditions also makes an important contribution to a successful outcome. Any plans for replacement of vegetation components and restoration of natural species diversity should include safeguards for preservation or enhancement of sand stability. The basic ecological requirements of the plant community cannot be circumvented but the speed of succession can be accelerated by thoughtful management of human and animal influence and the selection of species most likely to achieve priority objectives at each stage.

Failure to control grazing and browsing animals, particularly rabbits, probably constitutes the greatest threat to the New Zealand sand dune flora. Unless the activity of these animals is effectively controlled, restoration programmes based on native species are unlikely to be successful. Trampling and browsing will result in destruction or the reduction of growth rates. The ecological advantage will always be with the less heavily browsed and more vigorous members of the plant community. In the absence of species displaying the necessary vigour, deterioration of the vegetation cover and increased sand erosion are almost guaranteed.

Behind the current foredune, specific areas of bare sand exist where wind force and/or populations of browsing animals do not constitute a major threat to sand stability. In such locations (some east coast beaches; sheltered dune pockets on the west coast), the introduction of native sand dune plants described by Cockayne (1911) as "sand collectors" (e.g., species of *Coprosma*, *Pimelea*, *Cassinia*, *Kunzea*) can be attempted in planned and managed botanical restoration projects.

Where sand stability is more important than the immediate introduction of native species, it will be necessary to commence the revegetation process by selecting species known to be most vigorous and anatomically effective in that particular habitat. Planting should be as extensive as possible, as dense as possible, and as even as possible, the objective being rapid below-ground development and the establishment and maintenance of continuous cover over the largest possible area. On the seaward face of the current foredune the most effective species will be *S. sericeus*, and there will be no second successional stage. On bare sand (including drifts and blowouts) behind the crest of the current foredune, the most effective species will be *A. arenaria*, because it grows more vigorously in this habitat than any other sand-binding species and can withstand browsing. Treatment with nitrogenous fertiliser will be required at 6-monthly intervals to maintain maximum plant vigour. Once roots and rhizomes have permeated the sand, introduction of nitrogen-fixing species tolerant of wind and sand movement would reduce the need for fertiliser and speed up nitrogen and organic matter cycling processes (Gadgil *et al*. 1981). When there is sufficient shelter, sand dune plants such as *Cassinia* spp., *Coprosma acerosa*, and *Pimelea* spp. can be introduced and managed to restore the succession and the appropriate natural character and diversity of the vegetation. Examples of relatively undisturbed sand dune vegetation sequences in different regions of New Zealand have been described by Cockayne (1911), Smith *et al.* (1985), and Duguid (1990). Herbaceous plants, including *A. arenaria* and exotic nitrogen-fixing species, will eventually be shaded out by a dense canopy of taller plants. At this stage the nitrogen stored in stems, leaves, roots, and rhizomes will become available to other plants as decomposition progresses.

Dune areas without an extensive tree cover will always be vulnerable to sand erosion because herbaceous and shrubby plants are less likely to withstand the combined effects of human and animal activity. The effects on dry sand mobility exerted by coastal winds with a force typical of latitudes 30°–50°S can escalate rapidly, and often result in formation of large drifts. Although such drifts are a component of the current natural character of coastal dunes in New Zealand (Hesp 2000), they are often regarded as undesirable and in need of urgent management if they interfere with accepted human commercial activities or sites considered to have their own desirable attributes.

The activity of human beings can be regarded as an integral part of sand dune ecosystem processes. Continuous modification of dunelands through burning, grazing, introduction of exotic animals and plants, and recreational and urban use has, in many areas, reached the point of no return to the original natural state. Unrestricted human association is likely either to destroy dunelands completely by urbanisation, or to increase the threat of sand drift onto adjacent vegetated areas, wetlands, or neighbouring property by disturbance of the vegetation cover. Unless sand movement can be tolerated, management of the human influence must recognise the importance of a continuous, effective, vegetation cover. It must also encourage positive attitudes to the preservation of relatively small native vegetation communities that already exist on New Zealand's coastal dunes (Partridge 1992; Johnson 1992). Whether these result from natural establishment or from coastal planting programmes (e.g., Dahm 1994), active care is needed to ensure their sustainability.

Until sand mobility has been arrested, the most effective sand-binder is the only one that will be appropriate. In New Zealand, as in other countries, *A. arenaria* is the most effective known sand-binding grass for use in areas behind the seaward face of the current foredune. Judicious substitution of other successional species should be seen as a secondary objective, to be implemented only when an adequate degree of sand stability has been achieved. A research project set up to identify native species that can co-exist with or even suppress *A. arenaria* at this stage, without loss of overall vigour and effectiveness of the vegetation cover, is currently in progress.

The natural physical character of the sandy substrate of New Zealand's coastal dunes cannot be changed. Dry sand will continue to be subject to wind erosion whenever it is exposed. Where coastal managers consider sand drift to be a current or a potential problem, they must acknowledge that research and experience have demonstrated effective methods for minimising any destructive effects through the establishment of a continuous, vigorous, vegetation cover. These methods depend largely on the use of *A. arenaria*. Except on the seaward face of the current foredune, there is no evidence to suggest that any native species is more vigorous, less demanding, or better suited in any practical respect for use as the initial sand stabiliser.

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