SCREENING OF NITROGEN-FIXING PLANTS FOR USE IN SAND-DUNE REVEGETATION IN NEW ZEALAND

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ABSTRACT

Appropriate nitrogen-fixing plant species are required to replace *Lupinus arboreus* Sims, which once played an important nutritional role in the managed succession used to reclaim unstable coastal sand in New Zealand. A fungus disease has reduced *L. arboreus* populations by up to 95%.

Six spaced-plant trials at widely-separated locations on the west coast of the North Island identified 18 introduced species which are able to grow and fix nitrogen in the sand dune environment. Trials were conducted in the area immediately behind the foredune which is partially stabilised by sand-binding grasses. In this zone plant growth is limited by nitrogen supply.

Unless the activity of browsing animals on sand dunes can be controlled, only unpalatable species or those combining high tissue regeneration capacity with absence of weed potential are likely to be effective and acceptable substitutes for *L. arboreus*. The relative performance of the 18 species requires further examination under standard trial conditions before a final list can be recommended for sand revegetation purposes.

Keywords : coastal sand dunes; New Zealand; nitrogen deficiency; nitrogen fixation; revegetation.

INTRODUCTION

Plant growth on coastal sand dunes is limited by both physical and nutritional factors. The interaction of strong winds, summer drought, and substrate instability (lack of cohesiveness between dry sand particles) is sufficient to retard the growth of many species (Cockayne 1911). Willis (1963) found that the sparse and open character of the natural vegetation of sand dunes in North Devon, England, was attributable to severe deficiency of nitrogen and phosphorus. He considered that physical conditions were of secondary importance. In New Zealand, where the strong winds typical of latitudes 35° to 47°S probably have a greater physical impact, nutrient deficiency is also known to limit plant growth on coastal dunes. Local problems caused by low levels of micronutrients and sulphur (Will 1972; Gadgil *et al.* 1981) have been reported, but chronic nitrogen deficiency is the only nutritional factor known to characterise all unstable coastal sand in New Zealand (Hunter *et al.* 1991).

Between 1930 and 1987, the New Zealand Government acquired more than 115 000 ha of coastal dune land with sand drift problems. Successful stabilisation behind the seaward face of the foredune was achieved using methods based on Cockayne's (1911) perception that forestry would be the most permanent solution and the most appropriate end-use. Procedures designed to provide this permanent vegetation cover on mobile dunes involved firstly the planting of a sand-binding plant, *Ammophila arenaria* L. (marram grass), which was treated with nitrogenous fertiliser; secondly, the sowing of *Lupinus arboreus* (perennial tree lupin) to provide more ground cover and shelter; and finally, the planting of forest trees (usually *Pinus radiata* D. Don) on all except a coastal strip about 400 m wide (Fenton 1949; Wendelken 1974). *Lupinus arboreus* had been selected as a nitrogen-fixing plant which would be self-supporting in the dune environment and would contribute organic matter to the developing ecosystem. Its nutritional role in the managed plant succession was found to be more extensive than Cockayne (1911) had envisaged. Growth of marram grass and the productivity of *P. radiata* forest were found to be dependent on *L. arboreus* (Gadgil 1976; Jackson *et al.* 1983) which was capable of fixing at least 160 kg N/ha annually on the open dunes (Gadgil 1971b).

Lupinus arboreus, a native of California, was introduced to New Zealand during the last century and by 1906 was a common component of the dune flora (Cockayne 1906). Eighty years later Webb *et al.* (1988) described the species as a naturalised plant, locally common-to-abundant throughout New Zealand, and particularly well-established in coastal sandy sites. Thus, in the mid-1980s lupin formed a large proportion of the vegetation cover on the dunes and contributed a large amount of symbiotically-fixed nitrogen, much of which became available for uptake by other plants.

In the late 1980s, widespread death of lupin plants in the South Island was reported (Williams 1988). A fungus, *Colletotrichum gloeosporioides* (Penzig) Penzig et Saccardo, was identified as the causative agent and by 1993 the disease had spread throughout the country. This reduced lupin plant longevity and seed production and resulted in an estimated population reduction of 65–95% (Dick 1994). Very little recovery has been noted during the past 5 years.

Disappearance of the lupin is associated with reduction of vegetation cover and natural inputs of nitrogen. This was seen as a potential threat to the partially-stabilised (non-forested) coastal dune strip where exposure of sand to drought and wind will inevitably lead to dune erosion and rapid inland drift of sand. Fertiliser treatment is an expensive and inefficient method of supplying the nitrogen needed to maintain vegetation cover (Gadgil *et al.* 1981), and it was recognised that a nitrogen-fixing plant was needed to replace the lupin.

Douglas *et al.* (1994) described the 1991–92 establishment and first-year results of six screening trials set up to determine the performance of selected nitrogen-fixing species at representative dune sites on the west coast of the North Island. A brief reference to the trials was made by Ede *et al.* (1997) in an analysis of the role of nitrogen-fixing plants in sand dune stabilisation in New Zealand. This paper amplifies earlier results, provides a detailed account of the 1994 assessments, and summarises species performance during the first 3–4 years of the trials.

MATERIALS AND METHODS

Trial Establishment

Details of trial location, layout, and establishment procedures described by Douglas *et al.* (1994) are summarised in Tables 1 and 2. The six spaced-plant trials were conducted at four widely-separated locations. Most trials differed from each other in terms of species planted and establishment conditions. Common features included positioning in stands of marram grass and/or spinifex (*Spinifex sericeus* R. Br) just behind the foredune at each site. Randomised complete block layouts were used throughout. The experimental unit was a single-species plot of evenly-spaced transplants. Plots with square spacing were used in Trials A1–A5, but plots in Trial A6 consisted of single rows of plants.

Species Selection

Temperate nitrogen-fixing plant genera listed by Silvester (1976) and Allen & Allen (1981) were reviewed and rejections were made on the basis of the following factors, where known: susceptibility to *C. gloeosporioides*; large-tree habit; poisonous or prickly components; poor cover potential on infertile soils; lack of tolerance to drought; alpine or montane distribution. The 48 legume species in the native New Zealand flora, being less robust than many of their exotic counterparts (Silvester 1976) and rarely encountered in the sand dune environment (Johnson 1992; Partridge 1992) were excluded, together with the native nitrogen-fixing non-legumes, which are better adapted to moist sites or high altitudes (Silvester 1976).

Selection from the remaining 113 legume and 12 non-legume genera was made after discussions with New Zealand experts in the use of plants for revegetation purposes. Staff at the former Government research departments/units of the New Zealand Soil Conservation Centre, New Zealand DSIR Grasslands, and New Zealand Forest Research Institute were consulted. Final decisions were based on the availability of germplasm.

Local interest prompted the inclusion of *Casuarina glauca* Sieb., *Robinia pseudoacacia* L., and *Hippophae rhamnoides* L. in Trial A6 at Santoft, in spite of large tree and/or spiny habit. Twenty-six species of herbs, shrubs, and small trees, including *L. arboreus*, were thus included in one or more of the trials. All seedlings were raised under glasshouse conditions, inoculated with the appropriate *Rhizobium* strain soon after emergence, and hardened off before transplanting.

TABLE 1–Details of trial locations (after Douglas *et al.* 1994)

Location	Region	Approximate co-ordinates	Number of trials	Annual rainfall* (mm)	Mean air temperature (°C)*		Sand pH
					January	July	
Ninety-mile Beach	Northland	173°08′E 34°59′S	1 (A1)	1187	19.6	12.4	6.2–7.3
Kawhia Beach	Waikato	174°42′E 37°22′S	1 (A2)	1418	18.5	10.9	7.1
Harakeke Beach	Wanganui	175°05′E 40°02′S	1 (A3)	906	17.8	8.7	6.7
Santoft Beach	Manawatu	175°11′E 40°09′S	3 (A4, A5, A6)	874	17.1	8.0	8.1

* Long-term average from nearest meteorological station.

TABLE 2–Points of similarity and contrast between the 1991 and 1992 spaced-plant trials (after Douglas *et al.* 1994)

		Trial					
		A1 Ninety-mile Beach	A2 Kawhia Beach	A3 Harakeke Beach	A4 Santoft Beach	A5 Santoft Beach	A6 Santoft Beach
Trial establishment							
Established spring 1991		+	+	+	+	+	-
Established autumn 1992		-	-	-	-	-	+
Surrounded by rabbit-proof fencing		+	+	+	-	-	+
Seedlings raised in potting compost		-	-	-	+	+	+
Seedlings raised in local sand		+	+	+	-	-	-
Plant number per plot		36	36	20	8	8	10
Plant spacing (cm)		50×50	50×50	50×50	20×30	20×30	50
Number of replicated plots		4	4	3	3	3	4
Species and Accession No.*							
Acacia saligna H. Wendl.	FRI Nursery stock	+	+	+	-	-	-
	PMC 1684	-	-	-	-	-	+
Acacia sophorae (Labill.)	FRI Nursery stock	+	+	+	-	-	-
C. Martius.	PMC 3066	-	-	-	-	-	+
Astragalus cicer L.	AL 4325	-	-	-	+	+	+
Casuarina glauca Sieb.	PMC 3763	-	-	-	-	-	+
Chamaecytisus palmensis (Christ)	AL 3570	+	+	+	-	-	-
Bisby et K. Nicholls.	AL 3573	-	-	-	-	-	+
	AL 3820	-	-	-	-	-	+
	PMC 3552	-	-	-	+	+	+
Dorycnium hirsutum (L.) Ser.	AL 4278	-	-	-	+	+	+
Dorycnium pentaphyllum Scop.	AL 4289	-	-	-	-	-	+
Dorycnium rectum (L.) Ser.	PMC 1703	-	-	-	-	-	+

TABLE 2–cont.

		Trial					
		A1 Ninety-mile Beach	A2 Kawhia Beach	A3 Harakeke Beach	A4 Santoft Beach	A5 Santoft Beach	A6 Santoft Beach
Hedysarum coronarium L.	AL 3309	-	-	-	+	+	+
Hippophae rhamnoides L.	PMC 1900	-	-	-	-	-	+
Lathyrus japonicus Willd.	AL 3510	-	-	-	+	+	-
Lathyrus latifolius L.	AL 3525	+	+	+	-	-	-
	AL 3533	-	-	-	+	+	+
Lathyrus tuberosus L.	PMC 2839	-	-	-	+	+	-
Lespedeza cuneata G.Don.	AL 1612	+	+	-	-	-	-
Lotus corniculatus L.	S 2569	+	+	-	-	-	+
Lotus pedunculatus Cav.	ST 306	+	+	+	-	-	-
Lotus tenuis Waldst. et Kit. ex Willd.	S 2884	-	-	-	+	+	+
Lupinus arboreus Sims	AL 4294	-	-	-	+	+	-
Lupinus nootkatensis Donn.	AL 3167	+	+	+	-	-	-
Medicago arborea L.	PMC 1069	-	-	-	-	-	+
Robinia pseudoacacia L.	PMC 2724	-	-	-	-	-	+
Sutherlandia frutescens R. Br.	AL 4080	+	+	+	-	-	-
	PMC 3755	-	-	-	-	-	+
Teline stenopetala Webb et Berth.	AL 3374	+	+	+	-	-	-
Trifolium ambiguum Bieb.	AZ 2359	+	+	+	-	-	-
Vicia gigantea Hook.	PMC 931	-	-	-	-	-	+
Vicia sepium L.	PMC 3147	-	-	-	+	+	-

* Accession numbers for seed supplied by AgResearch Grasslands. Numbers relate to seed stock held at the Margot Forde Forage Germplasm Centre, Palmerston North, New Zealand.

Measurements and Statistical Analysis

In November (late spring) of each year from 1993 to 1995, plants in each plot were counted. Where the boundaries of the original individuals could not be identified, cover of the allocated space was assumed to indicate survival. Plants in each plot were scored for vigour on a scale of 1 (weak) to 5 (robust). Reproductive characteristics and evidence of damage or ill-health were recorded. Plant height and, where possible, maximum spread were measured. Assessments additional to those reported by Douglas *et al.* (1994) were conducted in November 1991, May 1992 (Trials A1–A3 only), and April 1993 (Trials A4–A6 only). Until 1993 (1994 in Trials A1–A3 only), herbage mass was estimated by harvesting the plant with height and spread closest to the plot mean and determining the oven-dry weight of live above-ground material. If parts of an individual plant extended beyond the boundary of the square allocated by spacing, an assumption was made that all plants in the plot had spread in a similar manner. In this case above-ground herbage (including that of neighbouring plants) was harvested from a vertical projection of the square in which plant height was closest to the plot mean. Relative nitrogenase activity in the roots of harvested plants was determined using an acetylene reduction technique (Hardy *et al.* 1973). Using the assumption that acetylene reduction activity was proportional to nitrogenase activity, species were ranked to show relative (rather than absolute) values at each trial site, a value of 100% being accorded to the species exhibiting maximum activity.

RESULTS

Within Trials A1–A3 and A6, 1994 data (measurements after 2.5–3 years' growth in the field) were subjected to analysis of variance and the Least Significant Difference test was used to compare the means. Data were transformed prior to analysis in order to achieve homogeneous variance and an error distribution closer to the normal distribution. Square root transformation was used for height and spread values, and $\log_e$ transformation for dry weight data. The 1994 data from Trials A4 and A5 were not amenable to analysis of variance due to the low numbers of survivors; for these trials means and their standard errors were calculated for measurements of each surviving species.

1994 Data from Specific Trial Sites, 2.5–3 Years After Establishment

(a) Trials A1–A3, Ninety-mile Beach, Kawhia, and Harakeke

Of the nine species common to all sites, five had survived at Ninety-mile Beach, six at Kawhia, and eight at Harakeke (Table 3). Several prostrate species had grown beyond the point where the original plants could be identified. In such situations it was assumed that cover of the square allocated to an individual indicated its survival. On this basis, plant survival (all nine common species) represented 17% (Ninety-mile Beach), 42% (Kawhia), and 18% (Harakeke) of the total planted. Overall plant vigour was lower at Ninety-mile Beach than at the other two sites.

Species with a plant vigour score of 4 or 5 at two of the three sites were *Acacia sophorae* (Labill.) C. Martius, *Lathyrus latifolius* L., and *Lotus pedunculatus* Cav. Maximum survival rate for *Lathyrus latifolius* plants was 2%. *Lotus pedunculatus* produced 10–28% cover at all sites but *A. sophorae* covered 54% and 88% of the available plot area at Ninety-mile Beach and Kawhia respectively. Species showing high vigour ratings at one site only were *Acacia saligna* H. Wendl. (Kawhia), *Chamaecytisus palmensis* (Christ) Bisby et K.Nicholls.

(Harakeke), and *Teline stenopetala* Webb et Berth. (Harakeke). The vigorous growth was associated with ground cover of 50% or more.

Between-site comparisons for individual species common to all sites indicated ($p<0.05$) that height growth was always least at Ninety-mile Beach, where species means never exceeded 55 cm. Within trials, *A. sophorae*, *C. palmensis*, and *T. stenopetala* were tallest at Harakeke, while *A. saligna* and *A. sophorae* were tallest at Kawhia.

Species with the highest combination of values for individual plant spread (plot cover) and survival rate were *A. sophorae* and *L. pedunculatus* at Ninety-mile Beach; *A. saligna* and *A. sophorae* at Kawhia; *C. palmensis* and *T. stenopetala* at Harakeke.

The greatest amount of above-ground dry matter was produced by *A. saligna* and *A. sophorae* at Kawhia, and *C. palmensis* and *T. stenopetala* at Harakeke. No statistical distinction could be made between surviving species on the basis of productivity at Ninety-mile Beach, despite mean dry matter yields for *A. sophorae* and *C. palmensis* that were 10 times the mass of the next highest-yielding species (*A. saligna*). Nitrogenase activity was highest in *L. pedunculatus* at Ninety-mile Beach, *A. sophorae* at Kawhia, and *T. stenopetala* at Harakeke.

Although no flowering or seedpod formation was observed at Ninety-mile Beach, both were evident at the other sites in all surviving species except *Trifolium ambiguum* Bieb. at Kawhia and Harakeke; *A. saligna*, *A. sophorae,* and *Sutherlandia frutescens* R.Br. at Harakeke. No seedlings were observed in any of the trials. Leaf necrosis and/or stem dieback were frequently observed at all three sites.

(b) Trials A4 and A5, Santoft Beach

Of the original 10 species planted, four had survived in Trial A4 and five in Trial A5 (Table 4). *Astragalus cicer* L. had the highest within-species survival rate in Trial A4, and *A. cicer*, *Lathyrus latifolius*, and *L. japonicus* Willd. in Trial A5 were the only species with a mean survival rate exceeding 20%. Here *A. cicer* showed the lowest between-plot variability. Plants of *L. japonicus* were observed in Trial A4 in spite of a previous zero survival record. All species in Trial A4 and *L. tuberosus* L. and *Lupinus arboreus* in Trial A5 were confined to one plot only. Highest vigour scores (4–5) were given to *A. cicer* and *Lathyrus tuberosus* in both trials, and *L. japonicus* in Trial A4.

Variability in plant height and spread was a feature of these trials. *Lupinus arboreus* produced the tallest and broadest individuals in Trial A4, but death from lupin blight was clearly imminent. In Trial A5, *Lathyrus latifolius* and *L. tuberosus* showed the greatest potential for individuals to contribute to ground cover, but *A. cicer* showed greater consistency in plant spread.

No harvesting was attempted due to low numbers of survivors. *Dorycnium hirsutum* (L.) Ser. and *L. latifolius* were flowering, but no seedlings were observed. As in previous years, evidence of browsing by rabbits and hares was apparent.

(c) Trial A6, Santoft Beach

Values for survival and vigour were both high for *A. cicer*, *Casuarina glauca*, and *Medicago arborea* L. (Table 5). Vigorous plants but lower survival rates were noted for *Chamaecytisus palmensis* (PMC 3552), *D. hirsutum*, *D. pentaphyllum* Scop., and *Lotus*

TABLE 3–Mean values for 1994 assessments of fenced Trials A1–A3 (3 years after planting).

Species	Survival: No. of individuals (%)	Survival: Plot cover (%)	Vigour (1=weak, 5=robust)	Plant height* (cm)	Plant spread* (cm)	Above-ground dry matter* (g/0.25 m²)	Within-trial relative nitrogenase activity (%)	Notes
Trial A1 — Ninety-mile Beach								
Acacia saligna	11 a†	ND	1 d	35 ab	44 a	48 a	0	Much dieback
Acacia sophorae	ND	54 a	3 b	47 a	ND	452 a	0	Some dieback, scorch.
Chamaecytisus palmensis	4 a	ND	2 c	54 a	82 a	496 a	0	Dieback above marram.
Lathyrus latifolius	0	–	–	–	–	–	–	–
Lespedeza cuneata	0	–	–	–	–	–	–	–
Lotus corniculatus	0	–	–	–	–	–	–	–
Lotus pedunculatus	ND	14 a	4 a	21 b	ND	15 a	100	A little dieback
Lupinus nootkatensis	0	–	–	–	–	–	–	–
Sutherlandia frutescens	0	–	–	–	–	–	–	–
Teline stenopetala	1 a	ND	3 b	33 ab	40 a	ND	ND	Dieback
Trifolium ambiguum	0	–	–	–	–	–	–	–
Trial A2 — Kawhia								
Acacia saligna	ND	90 a	4 a	210 a	ND	1544 a	<1	Flowers, seedpods; some scorch, a little dieback
Acacia sophorae	ND	88 a	5 a	183 a	ND	1703 a	100	Growing out of plot; seedpods; a little scorch
Chamaecytisus palmensis	1 a	ND	2 c	63 b	180 a	ND	ND	Seedpods; dieback - possibly browsed
Lathyrus latifolius	1 a	ND	4 a	63 b	175 a	ND	ND	In bud; some browsing
Lespedeza cuneata	0	–	–	–	–	–	–	–
Lotus corniculatus	0	–	–	–	–	–	–	–
Lotus pedunculatus	ND	28 b	3 b	24 b	ND	29 b	0	Flowers, seedpods; much scorch and dieback

TABLE 3–cont.

Species	Survival		Vigour (1=weak, 5=robust)	Plant height* (cm)	Plant spread* (cm)	Above-ground dry matter* (g/0.25 m^2)	Within-trial relative nitrogenase activity (%)	Notes
	No. of individuals (%)	Plot cover (%)						
Lupinus nootkatensis	0	–	–	–	–	–	–	–
Sutherlandia frutescens	0	–	–	–	–	–	–	–
Teline stenopetala	0	–	–	–	–	–	–	–
Trifolium ambiguum	5 a	ND	3 bc	7 b	10 a	1 c	ND	–
Trial A3 — Harakeke								
Acacia saligna	12 a	ND	2 a	95 bc	68 bc	71 b	24	Leaf curl
Acacia sophorae	ND	6 b	4 a	157 ab	ND	265 b	29	–
Chamaecytisus palmensis	ND	57 a	4 a	234 a	ND	3010 a	35	Flowers, seedpods
Lathyrus latifolius	2 a	ND	5 a	123 b	234 a	ND	ND	Flowers
Lotus pedunculatus	ND	10 a	4 a	44 cd	ND	ND	ND	In bud
Lupinus nootkatensis	0	–	–	–	–	–	–	–
Sutherlandia frutescens	2 a	ND	ND	52 bcd	33 cd	ND	ND	–
Teline stenopetala	ND	53 a	5 a	228 a	ND	2091 a	100	Flowers, seedpods; some dieback
Trifolium ambiguum	ND	3 b	2 a	21 d	ND	1 c	0	–

* Back-transformed means.

† For each site, values within a column followed by the same letter do not differ at the 5% significance level (LSD test)

ND = Not determined

TABLE 4—Mean values for1994 assessments of unfenced trials A4 and A5 at Santoft Beach. No destructive sampling was carried out in 1994.

Species	Trial A4 (2.5 years after planting)				Trial A5 (3 years after planting)				
	Survival (%)	Vigour (1=weak, 5=robust)	Plant height (cm)	Plant spread (cm)	Survival (%)	Vigour (1=weak, 5=robust)	Plant height (cm)	Plant spread (cm)	Notes
Astragalus cicer	17 (29)*	5	7	10	21 (19)	5	29 (1)	17 (4)	–
Chamaecytisus palmensis	0	–	–	–	0	–	–	–	–
Dorycnium hirsutum	0	–	–	–	13 (13)	3	37 (37)	40 (21)	Flowers; heavily browsed
Hedysarum coronarium	0	–	–	–	0	–	–	–	–
Lathyrus japonicus	4 (8)	4	2	2	0	–	–	–	–
Lathyrus latifolius	0	–	–	–	25 (43)	3	53 (46)	153 (209)	Flowers; leaf necrosis
Lathyrus tuberosus	4 (8)	5	7	5	21 (36)	4	29	106	Rhizomes spreading
Lotus tenuis	0	–	–	–	0	–	–	–	
Lupinus arboreus	4 (8)	3	80	55	4 (8)	2	69	ND	Mostly dead foliage
Vicia sepium	0	–	–	–	0	–	–	–	

( )* = Standard error
ND = Not determined.

TABLE 5–Mean values for the 1994 assessment of Trial A6, Santoft Beach (2.5 years after planting).

Species	Survival (%)	Vigour (1=weak, 5=robust)	Plant height* (cm)	Plant spread* (cm)	Above-ground dry matter* (g/0.5 m of row)	Within-trial relative nitrogenase activity (%)	Notes
Acacia saligna	70 ab†	3	105 a	95 bc	773 ab	13	Dieback above marram
Acacia sophorae	67 ab	3	92 ab	189 a	2391 ab	100	Suckering profusely; new shoots; some dieback and leaf tip necrosis
Astragalus cicer	70 ab	5	28 c	70 bc	10 c	<1	Rhizomes spreading
Casuarina glauca	86 a	4	29 c	14 d	2 c	0	Some leaves reddish; marram competing.
Chamaecytisus palmensis (AL 3573)	8 b	3	80 ab	87 bc	534 ab	49	Considerable leaf loss; one plot buried
Chamaecytisus palmensis (AL 3820)	17 b	3	54 bc	120 abc	536 ab	18	Chewed or browsed; dieback; prostrate growth
Chamaecytisus palmensis (PMC 3552)	8 b	4	83 ab	134 ab	ND	ND	Dieback; one plot buried
Dorycnium hirsutum	31 b	4	60 b	116 abc	317 ab	3	In full flower; marram competing; two plots buried
Dorycnium pentaphyllum	3 b	5	48 bc	58 c	ND	ND	Nearly all buried
Dorycnium rectum	25 b	3	86 ab	152 ab	298 ab	3	Seedlings; dieback; severe leaf necrosis at top; one plot buried
Hedysarum coronarium	14 b	2	49 bc	35 cd	ND	ND	A few seedlings; two plots buried
Hippophae rhamnoides	0	–	–	–	–	–	Two plots buried
Lathyrus latifolius	50 ab	3	64 ab	98 bc	16 bc	<1	Flowers; rhizomes spreading; leaf necrosis; two plots buried
Lotus corniculatus	36 b	5	33 bc	61 c	40 bc	<1	Seedlings; one plot buried
Lotus tenuis	58 ab	3	39 bc	123 abc	211 bc	9	Seedlings; some necrosis; one plot buried
Medicago arborea	78 ab	4	81 ab	104 bc	367 ab	1	Flowers; seedpods; leaf curl at tops; some chlorosis
Robinia pseudoacacia	22 b	3	67 ab	53 c	132 b	25	Slight leaf necrosis; two plots buried.
Sutherlandia frutescens	0	–	–	–	–	–	–
Vicia gigantea	0	–	–	–	–	–	–

* Backtransformed means

† For each column, values followed by the same letter do not differ at the 5% significance level (LSD test)

ND = Not determined.

corniculatus L. *Dorycnium pentaphyllum* plants had grown through sand which buried them in 1993 as well as sand deposited during 1994. Species with high survival rate but only moderate vigour were *Acacia saligna, A. sophorae, Lathyrus latifolius*, and *Lotus tenuis* Waldst. et Kit. ex Willd.

Species showing greatest ground-covering ability were *A. sophorae, C. palmensis* (AL 3820 and PMC 3552), *D. hirsutum, D. rectum* (L.) Ser., and *L. tenuis*. Above-ground dry matter production was highest for *A. saligna, A. sophorae, C. palmensis* (AL 3573 and AL 3820), *D. hirsutum, D. rectum*, and *M. arborea*. Greatest nitrogenase activity was observed in *A. sophorae*.

A few seedlings of *Hedysarum coronarium* L. were found and more than 50 seedlings of *D. rectum, L. corniculatus*, and *L. tenuis* were recorded within 1 m of the original plots allocated to these species. Leaf necrosis and stem dieback were common in this trial. Several plots had been inundated by sand on the seaward side of the site.

Overall Observations to 1995 (3.5–4 Years after Establishment)

Species persistence

Species/accessions represented by one or more plants for at least 3.5 years in fenced trials were *A. saligna, A. sophorae, Astragalus cicer, Casuarina glauca, Chamaecytisus palmensis* (AL 3570, 3573, 3820; PMC 3552), *D. hirsutum, D. pentaphyllum, D. rectum, H. coronarium, Lathyrus latifolius, Lotus pedunculatus, L. tenuis, M. arborea, R. pseudoacacia, T. stenopetala*, and *Trifolium ambiguum* (Tables 6–8).

Lespedeza cuneata G. Don and *Lupinus nootkatensis* Donn. plants all died soon after planting in the fenced trials. None of the plants in the unfenced trials persisted for more than 3 years; those with greatest longevity (3 years) were *A. cicer, D. hirsutum, Lathyrus latifolius, L. tuberosus*, and *Lupinus arboreus*.

Plant survival

Numbers of surviving plants varied with species, with trial conditions, and with time (Tables 6–8). *Acacia sophorae* had the highest overall survival/cover rate (100% in three out of four trials). Greater variability was demonstrated by *A. saligna* (100% and 12 % for 4 years at Kawhia and Ninety-mile Beach respectively) and *C. palmensis* AL 3570 (100% for 4 years at Harakeke; 2% for 2 years at Kawhia). Highest survival rates among other species were 59% for *Lathyrus latifolius* and 47% for *D. hirsutum* for 3.5 years at Santoft Beach. Approximately one-third of *Teline stenopetala* and *Trifolium ambiguum* plants survived to Year 4 at Harakeke. Six of the species planted in the fenced trial at Santoft Beach (*A. saligna, A. sophorae, Astragalus cicer, Casuarina glauca, Lotus tenuis*, and *M. arborea*) had survival rates of 70% or greater during the first year, but numbers declined thereafter.

In the unfenced Santoft Beach trials, a mean survival rate exceeding 30% was observed in five species (*Chamaecytisus palmensis, L. tenuis, A. cicer, D. hirsutum*, and *Lathyrus latifolius*) but for each this was sustained for only 1.5 years. *Astragalus cicer, L. latifolius*, and *L. tuberosus* achieved survival rates exceeding 20% for 3 years.

Vigour

At fenced sites plants of all species except *Lespedeza cuneata, Lupinus nootkatensis*, and *Vicia gigantea* Hook. received a vigour score of 3–5 (moderate to robust) in at least one assessment (Tables 6–8). *Acacia saligna, A. sophorae, C. palmensis*, and *Lotus pedunculatus* were moderately vigorous to robust at all fenced sites. Species that had died out or had low vigour scores (1–2) at some sites and high scores (3–5) at others were *Lathyrus latifolius, Lotus corniculatus, S. frutescens, Teline stenopetala*, and *Trifolium ambiguum*.

At the unfenced Santoft Beach sites, moderate-to-robust plants of all species except *H. coronarium* and *V. sepium* L. were noted in at least one trial. Low vigour scores were associated mainly with evidence of browsing by rabbits or hares.

Plant spread

Many species showed potential for spreading at least 1–2 m from the original planting position within 3.5–4 years. Those which spread more than 2 m in fenced trials were *A. saligna* at Kawhia, *A. sophorae* at Ninety-mile Beach and Kawhia, *C. palmensis* AL 3570 at Harakeke, *Lathyrus latifolius* at Kawhia, and *Teline stenopetala* at Harakeke. In unfenced trials only *L. latifolius* and *L. tuberosus* spread more than 1 m after 3 years. A mean spread of 235 cm was recorded for *Lupinus arboreus* plants in the second year after planting, but defoliation and death due to attack by *Uresiphita polygonalis maorialis* (Felder) (kowhai moth) and *Colletotrichum gloeosporiodes* was already causing a decline in vigour.

Nitrogenase activity

Many of the species exhibited nitrogenase activity 2–3 years after planting (Tables 6–8). Survival rates of *D. pentaphyllum* (plants inundated by sand), *Hippophae rhamnoides, Lathyrus japonicus, Lespedeza cuneata, V. gigantea*, and *V. sepium* were too low to allow destructive testing.

DISCUSSION

The trials were not designed to be part of a single investigation and, consequently, comparisons and conclusions are limited. The data do provide useful information about characteristics of the plant species used, and indications of the growth response of nitrogen-fixing plants in the sand dune environment. The seedling establishment phase was intentionally bypassed so that the potential of mature plants could be assessed and a larger number of species screened. Results, therefore, relate only to survival and growth of transplants.

Although Santoft Trials A4 and A5 were established 6 months earlier than Trial A6, planting methods were similar and comparisons between species common to the fenced and unfenced sites are legitimate. There is no doubt that the activity of rabbits and hares impeded plant growth in the unfenced Trials A4 and A5. Persistence data suggest that *Astragalus cicer, Lathyrus tuberosus*, and (diseased) *Lupinus arboreus* were least affected by adverse factors (including browsing) at the unfenced sites. Species common to Trials A4, A5, and A6 persisted for at least 3.5 years in the fenced trial but for only 3 years or less without fencing. Although the two unfenced trials probably attracted browsers, it is likely that where browsing animals are a component of the ecosystem, higher survival rates and productivity levels would be required from any palatable species used to provide adequate vegetation cover on sand dunes.

Plant size and growth rate of some species in the fenced trials exceeded those expected for *L. arboreus*. Under optimum conditions in its native (Californian) habitat, individual

TABLE 6–Persistence, plant vigour, nitrogenase activity, and sexual reproductive activity of species monitored in two or more fenced trials between 1991 and 1995. Values are trial means for each species.

Species		Trial	Persistence (years)	Highest survival rate (%)	Highest survival rate Period (yr)	Highest vigour score (1 = weak; 5 = robust)	Observed period of nitrogenase activity (yr)†	Reproductive structures
Acacia saligna		A1	4.0	12 C*	1.0-4.0	4	2.0	
		A2	4.0	100 C	4.0	4	3.0	Seed pods
		A3	4.0	21	1.0-2.0	4	3.0	
		A6	3.5	80	1.0	4	2.5	
Acacia sophorae		A1	4.0	100 C	3.0-4.0	4	2.0	
		A2	4.0	100 C	3.0-4.0	5	3.0	Seed pods
		A3	4.0	100 C	3.0-4.0	5	3.0	
		A6	3.5	73 C	1.5	4	2.5	
Chamaecytisus palmensis	AL 3570	A1	3.0	13	1.0	3	2.0	
	AL 3570	A2	3.0	2	1.0-2.0	4	2.0	Seed pods
	AL 3570	A3	4.0	100 C	3.0-4.0	4	3.0	Seed pods
	AL 3573	A6	3.5	10	1.0-1.5	4	2.5	Seed pods
	AL 3820	A6	3.5	20	1.5	5	2.5	
	PMC 3552	A6	3.5	18	1.0-1.5	5	1.5	
Lathyrus latifolius		A1	0.2	53	0.2	1	0.2	
		A2	4.0	50	0.2	4	0.2	Flower buds
		A3	4.0	35	0.2	5	0.2	Flowers
		A6	3.5	59	3.5	4	2.5	Seed pods
Lespedeza cuneata		A1	<0.2	–	–	–	ND	
		A2	<0.5	8	0.2	1	ND	
		A3	<0.2	–	–	–	ND	
Lotus corniculatus		A1	1.0	57	0.2	3	0.5	
		A2	2.0	16	1.0	2	2.0	
		A3	<0.2	–	–	–	ND	
		A6	1.5	48	1.0	5	2.5	Seedlings

TABLE 6–cont.

Species	Trial	Persistence (years)	Highest survival rate		Highest vigour score (1 = weak; 5 = robust)	Observed period of nitrogenase activity (yr)†	Reproductive structures
			(%)	Period (yr)			
Lotus pedunculatus	A1	4.0	11 C	1.0	4	3.0	
	A2	4.0	24 C	1.0-4.0	4	2.0	Seed pods
	A3	4.0	5 C	1.0-4.0	5	2.0	Flowers
Lupinus nootkatensis	A1	<0.2	–	–	–	ND	
	A2	0.2	9	0.2	1	0.2	
	A3	<0.2	–	–	–	ND	
Sutherlandia frutescens	A1	0.5	58	0.2	2	0.5	
	A2	1.0	83	0.2	4	0.5	
	A3	3.0	46	1.0	4	2.0	Seed pods
	A6	<1.0	–	–	–	ND	
Teline stenopetala	A1	4.0	18	1.0	4	2.0	Flowers
	A2	1.0	1	1.0	1	0.5	Seed pods
	A3	4.0	33 C	4.0	5	3.0	Seed pods
Trifolium ambiguum	A1	1.0	9	1.0	2	2.0	
	A2	3.0	27	1.0	3	2.0	
	A3	4.0	39 C	4.0	5	2.0	

* C = Individuals not distinguishable after Year 1; survival estimated as percentage of plot covered.
† No observations were made in 1995.
ND = Not determined—insufficient number of plants for destructive sampling.

TABLE 7–Persistence, plant vigour, nitrogenase activity, and sexual reproductive activity monitored at one fenced site only (Trial A6, Santoft Beach) between 1991 and 1995. Values are trial means for each species.

Species	Persistence (years)	Highest survival rate (%)	Highest survival rate Period (yr)	Highest vigour score (1 = weak; 5 = robust)	Observed period of nitrogenase activity* (yr)	Reproductive structures
Astragalus cicer	3.5	70	2.5	5	2.5	
Casuarina glauca	3.5	98	1.0	4	1.5	
Dorycnium hirsutum	3.5	47	3.5	5	2.5	Seedlings
Dorycnium pentaphyllum	3.5	8	1.0	5	ND	Flower buds
Dorycnium rectum	3.5	28	1.0–1.5	4	2.5	Flower buds
Hedysarum coronarium	3.5	48	1.5	4	1.5	Seedlings
Hippophae rhamnoides	1.5	10	1.0	4	ND	
Lotus tenuis	3.5	70	1.5	4	2.5	Seedlings
Medicago arborea	3.5	83	1.0	4	2.5	Seed pods
Robinia pseudoacacia	3.5	23	1.5	3	2.5	
Vicia gigantea	<1.0	–	–	–	ND	

* No observations were made in 1995.
ND = Not determined—insufficient number of plants for destructive sampling.

L. arboreus plants may reach a height and canopy diameter of 2 m (Davidson & Barbour 1977). In New Zealand, in the absence of lupin blight, a height of 1.45 m, width of 2.20 m, and above-ground dry weight of 1150 kg/ha was not uncommon in natural stands of lupin plants aged 3–4 years (A.M.Sandberg, pers. comm.). One or more of these dimensions was exceeded by *Acacia saligna, A. sophorae, C. palmensis, D. hirsutum, D. rectum, Lotus tenuis, M. arborea*, and *T. stenopetala* in the sand dune environment. Results from Trials A4 and A5 demonstrated the effect of disease on growth of *Lupinus arboreus*. A rapid, early growth rate is a desirable characteristic where there is urgent need for rapid development of ground cover, shelter, and organic matter input. This need must be balanced against the potential of fast-growing or fecund exotic species to become weeds. The presence of such plants is acceptable only if effective control measures can be easily enforced where necessary.

Species that failed during the first year in more than one of the fenced trials (*Lespedeza cuneata*, *Lupinus nootkatensis*) are unlikely to be useful in sand revegetation in New Zealand. Longevity of 1–3 years, noted in several of the trials, could be a useful attribute in mixtures containing other species with greater persistence but slower initial growth rates. Many plants failed during the first 2 years but considerable within-species variability was evident, one or two plants per plot showing a high degree of persistence even where most had died. In some species (*Lathyrus latifolius* in Trial A4, *D. rectum* in Trial A6) survival of underground rhizomes and roots allowed regeneration after apparent failure had been recorded.

Leaf necrosis and stem dieback occurred frequently. Many species exhibited active stem and leaf growth in less exposed positions on the plant and during the more favourable seasons. A sublethal degree of stress (such as browsing) may be beneficial to sand dune

TABLE 8–Persistence, plant vigour, nitrogenase activity, and sexual reproductive activity of species monitored in unfenced trials at Santoft Beach between 1991 and 1995. Values are trial means for each species.

Species & trial	Persistence (years)	Highest survival rate		Highest vigour score (1 = weak; 5 = robust)	Observed period of nitrogenase activity* (yr)	Reproductive structures
		(%)	Period (yr)			
Astragalus cicer						
A4	3.0	38	1.5	5	2.0	
A5	3.0	21	3.0	5	2.0	
Chamaecytisus palmensis						
A4	2.0	62	1.5	2	2.0	
A5	2.0	13	1.5–2.0	4	2.0	
Dorycnium hirsutum						
A4	2.0	8	2.0	4	2.0	Flowers
A5	3.0	33	1.5	5	2.0	Flowers
Hedysarum coronarium						
A4	2.0	4	2.0	2	1.0	
A5	<1.5	–	–	–	ND	
Lathyrus japonicus						
A4	2.5	4	2.5	4	ND	
A5	<1.5	–	–	–	ND	
Lathyrus latifolius						
A4	2.0	33	1.5	2	2.0	
A5	3.0	25	3.0	5	2.0	Flowers
Lathyrus tuberosus						
A4	2.5	4	2.5	5	1.0	
A5	3.0	21	3.0	4	2.0	
Lotus tenuis						
A4	2.0	48	1.5	4	1.0	
A5	2.0	4	2.0	3	ND	
Lupinus arboreus						
A4	3.0	27	1.5	3	2.0	
A5	3.0	13	2.0	3	2.0	Flowers
Vicia sepium						
A4	<1.5	–	–	–	ND	
A5	1.5	4	1.5	1	ND	

* No observations were made in 1994. No plants survived to November 1995.
ND = Not determined—insufficient number of plants for destructive sampling.

ecosystem development since continuous decay of tissues rich in nitrogen compounds and even compensatory stimulation of nitrogen-fixing mechanisms may ensue (Gadgil 1971a).

Nitrogenase activity was recorded in most species at one or more sites. The degree of activity was compared only at point time within each trial and then only in relative, rather than absolute, terms. On this basis, *A. sophorae* was the only species recorded as best performer in more than one trial in 1994 (Kawhia and Santoft A6). *Lotus pedunculatus* had the highest relative nitrogenase activity at Ninety-mile Beach and *T. stenopetala* at Harakeke.

Results from the A1–A3 trial series suggest that overall plant performance may have been enhanced by lower temperatures associated with higher latitude. Comparisons between the more northerly trials and those at Santoft are not strictly valid because Santoft trial material was planted in potting compost rather than sand.

Further detailed analysis of relative species performance in these trials is not justified. Combinations of characteristics relevant to sand dune stabilisation by revegetation can be compared only in trials with standardised layout and planting procedures. Of the 22 species (excluding *Lupinus arboreus*) which survived for more than 1 year in these trials, the following exhibited nitrogenase activity and would justify further examination:

Acacia saligna	*Acacia sophorae*
Astragalus cicer	*Casuarina glauca*
Chamaecytisus palmensis	*Dorycnium hirsutum*
Dorycnium rectum	*Hedysarum coronarium*
Lathyrus latifolius	*Lathyrus tuberosus*
Lotus corniculatus	*Lotus pedunculatus*
Lotus tenuis	*Medicago arborea*
Robinia pseudoacacia	*Sutherlandia frutescens*
Teline stenopetala	*Trifolium ambiguum*

Dorycnium pentaphyllum, Hippophae rhamnoides, Lathyrus japonicus, and *V. sepium* were not examined for nitrogenase activity and their exclusion from the above list may not be justified.

Some of the above species are likely to be effective candidates for replacing *Lupinus arboreus* in managed planting successions designed specifically to prevent unwanted movement of coastal sand. Experience with lupin has demonstrated that it is unwise to rely on a single species for the performance of an important role such as nitrogen supply to the ecosystem. In the sand dune context it will be necessary to investigate the successional dynamics of mixtures of nitrogen-fixing species, with the joint aims of maximising the amount/continuity of nitrogen inputs, and providing the best possible nursing system for species selected to complete the rehabilitation process.

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