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RELATIVE PERFORMANCE OF 18 NITROGEN-FIXING PLANT SPECIES AT THREE UNSTABLE COASTAL SAND DUNE SITES IN NEW ZEALAND

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ABSTRACT

Plant growth in unstable coastal sand is limited by nitrogen supply, and the promotion of *in situ* biological nitrogen fixation can reduce the need for fertiliser application where rapid growth of continuous vegetation cover is required after preliminary stabilisation with sand-binding species. *Lupinus arboreus* Sims (yellow tree lupin) was once used for this purpose, but susceptibility to a blight fungus has necessitated a search for alternative plant species.

Eighteen leguminous species raised in a nursery were transplanted into spaced-plant trials at three, widely separated, North Island west coast, sand dune sites. Trial areas were just behind the current foredune where planted *Ammophila arenaria* L.

(marram grass) or *Spinifex sericeus* R.Br (spinifex) was being used to commence the sand stabilisation process. Survival rates, growth characteristics, and nitrogen-fixing potential were compared over a period of 4.5 years (1993–97).

Assessments in the third year after planting gave mean values across all sites of 0–85% for survival, 7–121 cm for plant height, and 6–256 cm for plant spread (canopy diameter). Highest estimates of nitrogen accumulation in plant material in the fourth year were 38 kg/ha at Ninety Mile Beach (*Lathyrus latifolius* L.), 733 kg/ha at Muriwai Beach (*Dorycnium rectum* (L.) Ser.), and 869 kg/ha at Santoft Beach (*Medicago arborea* L.). Plants of 11 species survived for at least 5 years at all three sites.

Six of the species tested (*Dorycnium hirsutum* (L.) Ser., *D. pentaphyllum* Scop., *D. rectum*, *Lotus corniculatus* L., *L. pedunculatus* Cav., and *L. tenuis* Waldst. & Kit. ex Willd.) are recommended for use in the planting succession because they fix nitrogen and also grow at a moderate rate under a wide range of open dune conditions. Other species may be useful although more site-specific. Reliance on a single leguminous species for a continuous nitrogen supply should be avoided.

Keywords: coastal sand; nitrogen fixation; plant growth; species performance; nurse species; revegetation.

INTRODUCTION

Approximately 1090 km of the New Zealand coastline are bordered by potentially unstable sand dunes (Gibb 1983). During the twentieth century, 115 000 ha of sand drifting inland were stabilised by afforestation (Wendelken 1974). This involved successional planting — firstly, of a sand-binding species, *Ammophila arenaria*; secondly, of a nitrogen-fixing species, *Lupinus arboreus*; and finally, when a continuous herbaceous cover had developed, of *Pinus radiata* D.Don trees. Although the plantations were originally intended for protection, they developed into the highly productive and sustainable forests that now line many parts of the coast and extend inland in the Northland, Auckland, Waikato, Bay of Plenty, Manawatu, Nelson, and Canterbury regions.

Afforestation was recognised as the final stage of the sand stabilisation process (Cockayne 1911), trees having been identified as the dominant component of the natural climax community formed by undisturbed natural succession. The three-stage artificial plant succession was successful because it used specially adapted sand-binding plants to start the sand stabilisation process; because it incorporated nitrogen-fixing plants which improved the nutritional status of the chronically nitrogen-deficient ecosystem; and because trees provided the final protective canopy, deep stabilising root system, and organic matter input required for a self-sustaining vegetated ecosystem. Behind the current foredune crest a coastal strip approximately 500 m wide was usually left without trees because *A. arenaria* and *L. arboreus* were more tolerant of direct and frequent exposure to high winds, salt spray, and sand-blasting. An intact vegetation cover in this zone was maintained by constant vigilance and rapid replanting whenever sand became exposed as a result of storm events (Fenton 1949).

In the late 1980s, a fungal blight (*Colletotrichum gloeosporioides* (Penzig) Penzig & Saccardo) reduced *L. arboreus* populations throughout the country by 60–95% (Dick 1994). It became clear that the threat of sand migration inland from the non-forested coastal strip would be increased — firstly, because the physical contribution of *L. arboreus* to a continuous vegetation cover would be reduced and, secondly, because symbiotic nitrogen fixation and the addition of nitrogen-rich organic matter (Gadgil 1971c) would decrease to very low levels. The positive effect of *L. arboreus* on the vigour and growth of other species had already been demonstrated (Gadgil 1976, 1979). Unless alternative nitrogen-fixing species able to survive on coastal sand dunes could be identified, high costs were likely to be incurred in terms of either the extensive fertiliser treatment needed to maintain an adequate vegetation cover, or the effects of increased sand erosion and encroachment on to productive land.

Preliminary screening of nitrogen-fixing plants in several North Island locations identified 18 perennial species able to grow and fix nitrogen in partially stabilised sand immediately behind the current foredune (Douglas *et al.* 1994; Wanjiku *et al.* 1997; Gadgil, Douglas, Sandberg, Lowe & Foote 1999). This report presents the results of an intensive investigation designed to make direct comparisons between 15 of these species and to demonstrate their relative potential for growth and nitrogen fixation in standardised spaced-plant trials. Three additional species and two additional accessions of *Chamaecytisus palmensis* (Christ) Bisby et K.Nicholls were also examined. The overall objective was determination of the relative potential of these species for nitrogen accumulation, cover development, possible usefulness as nurse species, and potential weediness in the sand dune environment. Because the 48 nitrogen-fixing species of the native New Zealand flora are less robust than many of their exotic counterparts (Silvester 1976) and are not common in the sand dune environment (Johnson 1992; Partridge 1992), native nitrogen-fixers were not included in these trials.

MATERIALS AND METHODS

Trial Location and Site Characteristics

The sites selected for this study (from north to south — Ninety Mile Beach, Muriwai Beach, and Santoft Beach) covered a wide range of latitude on the west coast of the North Island of New Zealand and varied in annual rainfall and air temperature (Table 1). Sand at Santoft Beach was alkaline compared with sand at the other two sites, which were acidic/alkaline (Table 1). In each trial an area was chosen just behind the current foredune where active colonisation by the sand-binding grasses *Spinifex sericeus* and/or planted *Ammophila arenaria* had been in progress for at least 2 years, and the process of partial sand stabilisation had therefore begun. Plant species other than *A. arenaria* or *S. sericeus* were virtually absent from all sites in 1993.

At Ninety Mile Beach there was little protection from wind other than that afforded by planted *A. arenaria*/*S. sericeus*. In contrast, the Muriwai Beach site was sheltered by a high foredune. At Santoft Beach, dune orientation to prevailing winds resulted in some wind funnelling and consequent sand deposition. Browsing by rabbits or hares trapped inside the trial area was evident at Muriwai Beach in 1993 (the animals were promptly removed by local forestry staff).

Plant Material

Plants were grown in a nursery at Palmerston North during 1992–93 under standardised conditions and transplanted to the trial sites when aged at least 6 months. Plant preparation involved sowing seed of 18 nitrogen-fixing species (a total of 20 accessions; Table 2) in a

TABLE 1–Site details for the three spaced-plant trials.

Location	Region	Approximate coordinates	Annual rainfall* (mm)	Mean air temperature* (°C)		Sand pH
				January	July	
Ninety Mile Beach	Northland	173°08´E 34°59´S	1187	19.6	12.4	6.2–7.3
Muriwai Beach	Auckland	174°20´E 36°42´S	1328	18.4	10.4	6.5–6.8
Santoft Beach	Manawatu-Wanganui	175°11´E 40°09´S	874	17.1	8.0	8.1–8.2

* Long-term average from nearest meteorological station: Ninety Mile Beach 1967–80; Muriwai Beach 1948–80; Santoft Beach 1926–80 (NZ Met. Service 1983).

TABLE 2–Legume species and *Rhizobium* strains used.

Species	Accession No.*	Plant form	*Rhizobium* strain included for inoculation	Species from which *Rhizobium* was isolated
Acacia saligna H. Wendl.	PMC 3669	Woody shrub/tree	Macerated nodules obtained locally	*Acacia saligna*
Acacia sophorae (Labill.) C.Martius.	PMC 3066; 3066/2	Woody shrub/tree	Macerated nodules obtained locally	*Acacia sophorae*
Astragalus cicer L.	AL 4325	Herbaceous plant	NZP 5254	*Astragalus cicer*
Chamaecytisus palmensis (Christ) Bisby et K.Nicholls.	(a) AL 3211; 3218	Woody shrub/tree	NZP 5035	*Chamaecytisus palmensis*
	(b) AL 3573	Woody shrub/tree	NZP 5035	
	(c) AL 3820	Woody shrub/tree	NZP 5035	
Dorycnium hirsutum (L.) Ser.	AL 4278	Woody shrub	NZP 2235	*Lotus corniculatus*
Dorycnium pentaphyllum Scop.	AL 4289	Sub-shrub	NZP 2235	*Lotus corniculatus*
Dorycnium rectum (L.) Ser.	AL 4327	Shrub	NZP 2235	*Lotus corniculatus*
Hedysarum coronarium L.	AL 3309	Herbaceous plant	Commercial	
Lathyrus latifolius L.	AL 3533	Herbaceous plant	NZP 5470	*Lathyrus latifolius*
Lespedeza cuneata G.Don.	AL 495	Herbaceous plant	NZP 5049	*Macrotyloma africanum*
Lotus corniculatus L.	S 2569	Herbaceous plant	NZP 2196	*Lotus corniculatus*
Lotus pedunculatus Cav.	ST 306	Herbaceous plant	NZP 2309	*Lotus pedunculatus*
Lotus tenuis Waldst. & Kit. ex Willd.	S 2884	Herbaceous plant	NZP 2203	*Lotus tenuis*
Lupinus nootkatensis Donn.	AL 4242; 4243	Herbaceous plant	NZP 5214	*Lupinus angustifolius*
Medicago arborea L.	PMC 1069; 3541	Woody shrub	NZP 4021	*Medicago* sp.
Sutherlandia frutescens R. Br.	AL 3755; 4072; 4080	Shrub/small tree	NZP 5291	*Sutherlandia frutescens*
Teline stenopetala Webb & Berth.	AL 3371	Woody shrub/tree	NZP 5032	*Cytisus scoparius*
Trifolium ambiguum Bieb.	AL 2640	Herbaceous plant	Commercial	

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

sand/pumice mixture contained in polystyrene trays. When 1.5–2.0 cm tall, seedlings were inoculated with selected *Rhizobium* strains. A pure culture of each strain was prepared on yeast-mannitol agar from samples which had been freeze-dried and vacuum-sealed in ampoules. A suspension containing a mixture of all strains was watered on to all seedlings except *Trifolium ambiguum* Bieb. and *Hedysarum coronarium* L., to which a mixture of commercial peat-based strains for *Trifolium* spp. and *H. coronarium* was applied. All seedlings in a random sample from each species were nodulated when checked later and all plants had green foliage.

A separate study (Gadgil, Sandberg & Lowe 1999) has established that long-term plant performance on the dunes is not significantly influenced by the choice of potting compost, rather than sand, as the nursery rooting medium. Seven to 10 days after inoculation, seedlings were transferred into potting compost (1/9 pumice, 5/9 peat, and 1/3 bark) mixed with fertiliser (0.7 g N, 0.4 g P, 0.4 g K, 1.2 g Ca, 0.5 g Mg, and 0.3 g S per bag) contained in PB3/4 plastic planter bags (6 × 6 × 10 cm high) at the rate of one seedling per bag. They were watered sparingly as required and kept in an unheated plastic tunnel-house for 2–3 weeks before being transferred to a gravel-based outdoor storage area. A fungicidal spray (Benlate: a.i. benomyl, 500 g/kg) was applied every 3–4 weeks. All plants were 5–20 cm tall and in apparent good health at time of transplanting on to the dunes.

Trial Layout

The trial at each site consisted of six randomised complete blocks of 20 single-species/accession plots. Each plot (experimental unit) was a row of 15 plants at 30 cm spacing, located between rows of *Spinifex sericeus* or *Ammophila arenaria* and separated from the next plot by at least 1 m. Plants were allocated to blocks on the basis of size (height and spread) so that Block 1 contained the smallest and Block 6 the largest plants of each species/accession at the time of transplanting. Overall distribution of plant size was similar at each site.

Transplanting

Starting at Ninety Mile Beach and working southwards, transplanting on to the dunes was carried out during the period late April–early June 1993. The plastic bag was removed and the intact root ball was buried in a freshly dug hole so that compost and roots were completely covered with sand. Each trial was enclosed with rabbit-proof netting.

Measurements and Assessments

From 1993 to 1997, measurements were made annually between late October and early December, starting at Ninety Mile Beach and staggering dates so that all plants had been in the field for the same length of time when measured. Plant vigour was assessed by assigning a Vigour Index value to each plot. Index values ranged from 1 (= weak; very unhealthy appearance) to 5 (= robust; excellent healthy appearance) and provided a subjective assessment of the combined effects of adverse factors such as salt windburn, heat, drought, disease, and damage by insects and other browsers. Height and spread (canopy diameter measured at right angles to the planting line) of each surviving plant were measured and the individual with dimensions nearest to the row mean was harvested for determination of above-ground dry matter production (litter excluded). Wherever possible at least two individuals per row were retained for further observation of persistence. Harvested material was dried in forced-draught ovens at 70ºC to constant weight. Plant spacing dimensions and mean dry weight/plant were used to estimate above-ground dry matter production on a kilograms per hectare basis.

In 1996, two plants per species with an immediate neighbour on either side were harvested from each site. Above- and below-ground material was dried, weighed, and ground to pass through a 1-mm sieve. Roots were washed before drying. The nitrogen concentration of the ground material was determined, using methods described by Nicholson (1984). Nitrogen content per plant was calculated as nitrogen concentration multiplied by dry weight per plant and used together with plant spacing dimensions to estimate nitrogen accumulation on a kilograms per hectare basis.

Estimates of relative nitrogenase activity in the roots were made in 1993, 1994, and 1995 by means of an acetylene reduction technique (Hardy *et al.* 1973). Immediately after removal of the above-ground material of harvested plants, a metal corer (108 mm diameter × 85 mm deep) was used to excavate root material in Blocks 5 and 6 of each trial. Roots of each plant were placed in a sealed glass jar from which 100 ml of air was removed and replaced with freshly prepared acetylene. After 30 min incubation in the shade, two 4-ml gas samples were withdrawn from the jar and transferred to the laboratory for ethylene analysis. Working on the assumption that acetylene reduction activity was proportional to nitrogenase activity, species were ranked to show relative (rather than absolute) nitrogen fixation potential at each trial site, a value of 100% being accorded to the species which exhibited maximum activity at that site. Comparisons of absolute activity rates across trial sites were not attempted because the acetylene reduction assay is sensitive to temperature, moisture level, and light intensity (Bergersen 1980).

Presence or absence of seedlings within 1 m of the original plant row was noted. When the original individual plants became difficult to distinguish from each other, height and spread of live plant material at a selected position in a row were recorded. For determination of dry matter production in such cases, two boundary lines, each 15 cm from the original plant position, were marked at right angles to the row. All above-ground plant material lying between vertical projections of these lines was harvested. The number of harvested plants was taken into account during the calculation of survival rates.

At the request of the managers of adjacent land, species considered to have weed potential (*Acacia saligna* H.Wendl., *A. sophorae* (Labill.) C.Martius) were removed from the trials after the November 1995 assessments. At the same time, any experimental plants likely to interfere with those in adjacent rows were trimmed.

Statistical Analysis

Results of the 1995 assessment (2.5 years after planting) were selected for examination of species and site effects on plant growth and vigour. This data set described the latest stage in the trial at which comparisons between all species/accessions were possible. The following variables were analysed: survival percentage, spread, height, vigour, and above-ground dry weight. Analysis of variance was used to test the significance of species differences, and pairwise comparisons between means for individual species were made with least significant difference (LSD) tests. Using the SAS procedure MIXED (SAS Institute 2000), separate analyses were performed for each site. Overall analyses across all sites, including tests for interactions between site and species, were also performed.

Distributions of height, spread, and above-ground dry weight were positively skewed. Also, variances were not homogeneous across all species, but were larger for the more productive species. For height and spread, the square root transformation was found suitable for achieving distributions close to normality and with homogeneous variance, while the log transformation was used for dry weight. The arcsine transformation was used when analysing percentage survival. Although analyses were performed on transformed data, actual means are presented in the Results section.

RESULTS

Large amounts of data were collected during the 4.5-year term of the study and these are available from the authors if more information is required about the detailed performance of any species/accession at any of the three sites. The following account draws attention to broader outcomes.

Plant Survival

Several species failed during the 4.5-year observation period (Table 3). *Lespedeza cuneata* G.Don., *Lupinus nootkatensis* Donn., *Sutherlandia frutescens* R.Br., and *Trifolium ambiguum* eventually disappeared from all three sites; *Hedysarum coronarium* from two sites; *Chamaecytisus palmensis* (b) and (c) and *Medicago arborea* from one site only.

Seedling Production

During the 4.5-year observation period, seedlings of 14 of the planted species were found within 1 m of the planted rows. Overall, fewer rows had associated seedlings at Ninety Mile Beach (12) than at Muriwai Beach (19) or Santoft Beach (30). Species producing seedlings at all three sites were *Dorycnium hirsutum*, *D. pentaphyllum*, *Lotus corniculatus*, *L. tenuis*, and *Teline stenopetala* Webb & Berth. Estimates of seedling numbers were found to be unreliable and are not reported.

TABLE 3–Year of disappearance of planted legume species from the three spaced-plant trials between 1993 and 1997.

Year	Ninety Mile Beach	Muriwai Beach	Santoft Beach
1993	*Lespedeza cuneata* *Sutherlandia frutescens*	–	–
1994	*Chamaecytisus palmensis (b)* *Lupinus nootkatensis* *Trifolium ambiguum*	*Lupinus nootkatensis*	*Lespedeza cuneata*
1995	*Astragalus cicer*	*Sutherlandia frutescens*	*Lupinus nootkatensis* *Sutherlandia frutescens*
1996	*Teline stenopetala*	*Medicago arborea* *Trifolium ambiguum*	*Trifolium ambiguum* *Hedysarum coronarium*
1997	*Hedysarum coronarium*	*Lespedeza cuneata*	*Chamaecytisus palmensis (c)*

Nitrogen-fixing Potential

At least 10 species at Ninety Mile Beach, 15 at Muriwai Beach, and 15 at Santoft Beach were actively fixing nitrogen 2.5 years after planting (Table 4). Of these, *Lathyrus latifolius* showed greatest activity at Ninety Mile Beach and Santoft Beach, *Hedysarum coronarium* at Muriwai Beach.

TABLE 4–Relative acetylene reduction rates recorded for legume species at three sites in 1995 (2.5 years after planting). For each site ethylene production is expressed as a percentage of the highest value recorded.

Species	Ninety Mile Beach	Muriwai Beach	Santoft Beach
Acacia saligna	<1	23	8
Acacia sophorae	74	17	48
Astragalus cicer		<1	<1
Chamaecytisus palmensis (a)		2	<1
Chamaecytisus palmensis (b)		1	2
Chamaecytisus palmensis (c)		4	<1
Dorycnium hirsutum	5	<1	<1
Dorycnium pentaphyllum	24	<1	3
Dorycnium rectum	6	<1	2
Hedysarum coronarium	6	100	
Lathyrus latifolius	100	5	100
Lotus corniculatus	5	6	3
Lotus pedunculatus	67	2	2
Lotus tenuis	15	<1	<1
Medicago arborea			2
Teline stenopetala		<1	8

One year later, estimates of total nitrogen accumulation in legume plant material (Table 5) showed little correlation with the 1995 acetylene reduction assay results. Data obtained for four species at Ninety Mile Beach, seven at Muriwai Beach, and 11 at Santoft Beach indicated that by the fourth year those accumulating the greatest amount of nitrogen were *Lathyrus latifolius* at Ninety Mile Beach, *Dorycnium rectum* at Muriwai Beach, and *Medicago arborea* at Santoft Beach. Species which had accumulated at least 120 kg N/ha were *Dorycnium pentaphyllum, D. rectum*, *Lathyrus latifolius*, *Lotus corniculatus*, and *L. tenuis* at Muriwai Beach; *Chamaecytisus palmensis (a)*, *Dorycnium hirsutum*, *D. pentaphyllum*, *Lathyrus latifolius*, and *Medicago arborea* at Santoft Beach.

Statistical Analysis of Data Collected in 1995 (2.5 Years after Planting)

Highly significant differences between species in terms of plant survival, spread, and height were found at all sites. The combined analysis across all sites confirmed the strong differences between species in survival, spread, height, dry weight, and vigour, but also indicated that there were significant species-by-site interactions for each of these attributes (Table 6).

TABLE 5–Nitrogen accumulation (kg/ha) by legume species at three sites in 1996 (3.5 years after planting). Values are means for two representative plants per site. The shaded area denotes trimmed plants.

Species	Ninety Mile Beach			Muriwai Beach			Santoft Beach		
	Above-ground	Below-ground	Total	Above-ground	Below-ground	Total	Above-ground	Below-ground	Total
Astragalus cicer							44	9	52
Chamaecytisus palmensis (a)							320	20	341
Chamaecytisus palmensis (c)							40	2	42
Dorycnium hirsutum	17	6	23	83	10	93	228	20	247
Dorycnium pentaphyllum				103	24	126	141	27	168
Dorycnium rectum	5	22	27	467	266	733	23	18	40
Lathyrus latifolius	8	30	38	140	186	325	63	82	144
Lotus corniculatus				57	97	154	13	18	32
Lotus pedunculatus	1	8	9	41	3	44	20	17	36
Lotus tenuis				46	85	131	36	14	51
Medicago arborea							783	86	869

TABLE 6–Results of significance tests from combined analysis of variance across all sites. Analyses were conducted on transformed data for survival (arcsine), spread (square root), height (square root), and dry weight (log).

Source of variation	Survival		Spread		Height		Dry weight		Vigour	
	F-test	Prob	F-test	Prob	F-test	Prob	F-test	Prob	F-test	Prob
Site	$F_{2,15}$=23.02	<0.0001	$F_{2,15}$=5.30	0.018	$F_{2,15}$=27.64	<0.0001	$F_{2,14}$=6.68	0.0092	$F_{2,15}$=10.07	0.0017
Species	$F_{19,272}$=36.83	<0.0001	$F_{18,160}$=22.46	<0.0001	$F_{18,160}$=45.77	<0.0001	$F_{16,114}$=20.81	<0.0001	$F_{18,160}$=10.77	<0.0001
Species × site	$F_{38,272}$=4.74	<0.0001	$F_{28,160}$=8.00	<0.0001	$F_{28,160}$=5.49	<0.0001	$F_{18,114}$=2.34	0.036	$F_{28,160}$=5.65	<0.0001

Plant Survival

Although the number of species with some plants surviving at least into the fifth year was similar at all sites (Ninety Mile Beach 12, Muriwai Beach 15, Santoft Beach 14), relative survival in 1995 was quite variable (Table 7) and was influenced by species and by site location. For instance, *Dorycnium hirsutum* and *Acacia sophorae* survived best across all sites, but at Muriwai Beach four other species ranked higher for survival than *A. sophorae.*

TABLE 7–Mean survival (%) of legume species at three sites in 1995 (2.5 years after planting). Values within a column followed by the same letter do not differ significantly (LSD test; α=0.05). Statistical analyses were performed on transformed data, but actual means are shown for clarity. Legumes are ranked from highest to lowest survival across all sites.

Species	Ninety Mile Beach	Muriwai Beach	Santoft Beach	All sites
Dorycnium hirsutum	52.7 ab	100.0 a	98.7 a	84.7 a
Acacia sophorae	74.4 a	78.9 abcd	97.4 a	83.6 a
Lotus pedunculatus	41.0 bc	98.7 a	94.9 a	78.2 ab
Lathyrus latifolius	36.9 bc	100.0 a	91.0 a	76.0 ab
Dorycnium rectum	46.3 b	92.3 ab	83.3 ab	74.0 abc
Lotus corniculatus	21.8 bcd	100.0 a	73.1 abc	65.0 abcd
Lotus tenuis	25.2 bc	79.9 abcd	82.1 ab	62.4 bcde
Dorycnium pentaphyllum	13.1 cd	84.6 abc	85.4 ab	61.0 cde
Chamaecytisus palmensis (a)	16.6 cd	94.9 ab	56.5 bc	56.0 de
Acacia saligna	36.8 bc	73.1 bcd	57.6 bc	55.8 de
Chamaecytisus palmensis (c)	41.7 bc	65.0 cd	58.6 bc	55.1 def
Teline stenopetala	0.0 d	100.0 a	49.8 c	49.9 ef
Chamaecytisus palmensis (b)	0.0 d	61.7 d	58.6 bc	40.1 fg
Hedysarum coronarium	24.1 bc	56.4 d	5.1 g	28.5 gh
Astragalus cicer	0.0 d	9.2 e	51.1 c	20.1 h
Medicago arborea	23.1 cd	1.7 e	33.3 c	19.4 hi
Trifolium ambiguum	0.0 d	5.1 e	5.2 g	3.5 ij
Lespedeza cuneata	0.0 d	2.8 e	0.0 g	0.9 j
Sutherlandia frutescens	0.0 d	0.0 e	1.2 g	0.4 j
Lupinus nootkatensis	0.0 d	0.0 e	0.0 g	0.0 j

Plant Height

Exposure of plant parts above the level of surrounding *Ammophila arenaria*/*Spinifex sericeus* plants frequently resulted in necrosis associated with salt windburn. Tallest species overall were *Chamaecytisus palmensis* (a and b) and *Teline stenopetala,* with heights that were not significantly different from each other (Table 8). Five species had reached a mean height of more than 1 m at Muriwai Beach, but only one at Santoft Beach. At Ninety Mile Beach the tallest species was *Acacia sophorae* with a mean height of 46 cm.

TABLE 8–Mean height (cm) of legume species at three sites in 1995 (2.5 years after planting). Values within a column followed by the same letter do not differ significantly (LSD test; α=0.05). Statistical analyses were performed on transformed data, but actual means are shown for clarity. Legumes are ranked from greatest to least mean height across all sites.

Species	Ninety Mile Beach	Muriwai Beach	Santoft Beach	All sites
Chamaecytisus palmensis (b)		134.8 a	109.6 a	120.8 a
Teline stenopetala		129.6 a	81.9 ab	107.9 ab
Chamaecytisus palmensis (a)	27.3 bc	138.5 a	93.7 a	103.4 ab
Acacia saligna	25.8 bc	118.2 a	94.4 a	86.2 b
Dorycnium rectum	32.3 b	127.3 a	40.7 d	68.8 c
Acacia sophorae	46.0 a	71.0 b	69.0 bc	62.0 c
Chamaecytisus palmensis (c)	26.0 bc	77.3 b	52.8 cd	55.3 cd
Dorycnium hirsutum	29.9 b	65.1 b	55.6 cd	51.9 cd
*Sutherlandia frutescens**			45.0	45.0
Medicago arborea	29.8 b	27.0 de	56.2 cd	44.5 cd
Lathyrus latifolius	17.8 cd	69.3 b	40.9 d	42.7 d
Hedysarum coronarium	15.8 cd	59.2 bc	20.2 e	40.7 d
Dorycnium pentaphyllum	13.7 de	40.7 d	38.3 d	35.8 d
Lotus tenuis	15.2 d	35.3 d	35.3 d	29.4 d
Lotus pedunculatus	8.0 e	45.1 cd	33.5 d	28.9 d
Lotus corniculatus	12.8 de	33.9 d	14.6 e	22.0 e
Lespedeza cuneata		11.5 ef		11.5 f
Astragalus cicer		5.9 fg	10.0 e	9.0 f
Trifolium ambiguum		1.7 g	14.2 e	6.7 f

* Survival too low to allow inclusion in LSD comparisons.

Plant Spread (Ground Coverage)

Stronger development of lateral shoots often occurred where height growth was inhibited by salt windburn. An extreme example was seen at Ninety Mile Beach where *Chamaecytisus palmensis* (c) attained a mean spread of 221 cm but a height of only 26 cm (Tables 8 and 9). Over all sites, *Acacia sophorae* showed the greatest propensity for ground coverage (Table 9). At Muriwai Beach, five other species had higher mean values for plant spread. Greatest mean plant width (472 cm) recorded for *Acacia sophorae* at Ninety Mile Beach was twice that of any other site/species combination. Muriwai Beach had more species with spread exceeding 1 m (11) than either Ninety Mile Beach (four) or Santoft Beach (two).

Plant Vigour

Dorycnium hirsutum was the only species with a mean Vigour Index value of 4.0–5.0 (robust) at all three sites (Table 10). In total, there were five species within this vigour range at Ninety Mile Beach, seven at Muriwai Beach, and six at Santoft Beach.

Above-ground Dry Matter Production

Where measured, above-ground dry matter production across all sites varied between 1 and 1998 kg/ha, highest values being associated with woody species (Table 11).

TABLE 9–Mean spread (cm) of legume species at three sites in 1995 (2.5 years after planting). Values within a column followed by the same letter do not differ significantly (LSD test; α=0.05). Statistical analyses were performed on transformed data, but actual means are shown for clarity. Legumes are ranked from greatest to least spread across all sites.

Species	Ninety Mile Beach	Muriwai Beach	Santoft Beach	All sites
Acacia sophorae	472 a	140 bcde	155 a	256 a
Teline stenopetala		235 a	83 bcd	166 b
Chamaecytisus palmensis (a)	188 bc	213 ab	99 bc	160 b
Chamaecytisus palmensis (c)	221 b	133 bcde	89 bcd	138 bc
Chamaecytisus palmensis (b)		176 abcd	95 bcd	131 bc
Dorycnium rectum	67 de	205 abc	58 de	113 cd
Lathyrus latifolius	63 de	170 abcd	75 cd	103 cd
Dorycnium hirsutum	77 cde	104 defg	110 b	99 cd
Acacia saligna	56 de	113 def	86 bcd	89 cd
Medicago arborea	125 bcd	10 hi	86 bcd	86 cd
Lotus pedunculatus	53 de	133 cde	69 d	85 d
*Sutherlandia frutescens**			82	82
Hedysarum coronarium	61 de	110 defg	34 ef	80 d
Dorycnium pentaphyllum	52 de	87 efg	83 bcd	80 d
Lotus tenuis	33 e	58 gh	57 de	51 d
Lotus corniculatus	34 e	65 fgh	26 f	43 d
Astragalus cicer		25 hi	24 f	24 de
Trifolium ambiguum		3 i	21 f	10 e
Lespedeza cuneata		6 i		6 e

* Survival too low to allow inclusion in LSD comparisons.

DISCUSSION

Site Effects

Care had been taken to standardise seedling preparation, planting techniques, and plot layout, and it can be assumed that between-site differences in species performance were related largely to differences in local climate and sand characteristics (at least pH). Since sites were chosen for disparity in terms of geographic latitude, degree of shelter, and density of existing vegetation, species/site interactions were expected and these were clearly demonstrated. Ability to fix nitrogen at all three sites (Table 4) and to persist into the fifth year implies tolerance of a wide range of coastal conditions, an attribute exemplified by *Lupinus arboreus* (Wendelken 1974) and shared by *Dorycnium hirsutum, D. pentaphyllum, D. rectum, Lathyrus latifolius, Lotus corniculatus, L. pedunculatus,* and *L. tenuis.*

Contribution to the Nitrogen Status of the Ecosystem

Any well-established nitrogen-fixing plant tolerant of conditions on semi-stable coastal dunes can be assumed to be self-sufficient in terms of nitrogen supply. The nitrogen content of decomposing tissues added to the environment through litterfall or mortality is likely to be higher than that of non-nitrogen-fixing species (Maron & Jefferies 1999; Martinez &

TABLE 10–Mean Vigour Index values for legume species at three sites in 1995 (2.5 years after planting). Values within a column followed by the same letter do not differ significantly (LSD test; α=0.05). Statistical analyses were performed on transformed data, but actual means are shown for clarity. Legumes are ranked from greatest to least mean vigour across all sites.

Species	Ninety Mile Beach	Muriwai Beach	Santoft Beach	All sites
Dorycnium hirsutum	4.0 a	5.0 a	4.5 a	4.5 a
Dorycnium pentaphyllum	3.5 ab	4.7 ab	4.2 ab	4.3 ab
*Sutherlandia frutescens**			4.0	4.0
Lotus corniculatus	4.0 a	4.2 bcd	3.7 bc	3.9 b
Lotus tenuis	4.0 a	3.7 cde	4.0 abc	3.9 b
Astragalus cicer		2.5 fgh	4.2 ab	3.8 b
Acacia sophorae	4.0 a	4.0 bcd	3.5 c	3.8 b
Lotus pedunculatus	3.8 a	4.3 abc	3.2 cd	3.8 b
Medicago arborea	4.0 a	1.0 h	4.0 abc	3.6 b
Dorycnium rectum	3.4 ab	4.3 abc	3.0 cde	3.6 b
Hedysarum coronarium	3.5 ab	3.7 cde	2.3 ef	3.3 bc
Lathyrus latifolius	2.8 b	3.7 cde	3.3 cd	3.3 bc
Acacia saligna	2.8 b	3.7 cde	3.0 cde	3.2 cd
Teline stenopetala		4.0 bcd	1.6 f	2.9 cd
Chamaecytisus palmensis (c)	3.5 ab	3.0 ef	2.0 f	2.8 cd
Chamaecytisus palmensis (a)	3.0 b	3.8 cde	1.7 f	2.8 cd
Chamaecytisus palmensis (b)		3.5 def	2.0 f	2.7 cd
Lespedeza cuneata		2.5 fg		2.5 cd
Trifolium ambiguum		2.0 gh	2.5 def	2.2 d

* Survival too low to allow inclusion in LSD comparisons.

Garcia-Franco 2004; Yelenik *et al.* 2004) and will make a greater contribution to the nitrogen status of a chronically nitrogen-limited community such as that found in the coastal sand dune ecosystem.

In this study, limited resources and the well-known shortcomings of the acetylene reduction assay method (Bergersen 1980) mean that data for relative potential nitrogen input are far from complete. The nitrogen content of living legume tissue could be calculated only where there was sufficient material for harvesting. Here it provided a minimum estimate of relative nitrogen accumulation, because data for nitrogen in litter and nitrogen taken up from decomposition products by associated plants were not included. Several species were shown to be capable of accumulating at least as much nitrogen as healthy *Lupinus arboreus* in the fourth year after planting. Data of Gadgil (1976) indicated an increase of 120 kg N/ha attributable to the presence of *L. arboreus* in the understorey of a 4-year-old *Pinus radiata* sand dune forest near Muriwai Beach. On the single criterion of nitrogen accumulation, therefore, the following species could be considered as replacements for *L. arboreus* in a sand dune revegetation succession: *Dorycnium pentaphyllum, D. rectum*, *Lathyrus latifolius*, *Lotus corniculatus,* and *L. tenuis* at Muriwai Beach; *Chamaecytisus palmensis (a)*, *Dorycnium hirsutum*, *D. pentaphyllum*, *Lathyrus latifolius,* and *Medicago arborea* at Santoft Beach. At Ninety Mile Beach the maximum nitrogen accumulation

TABLE 11–Above-ground dry weight (kg/ha) of legume species at three sites in 1995 (geometric means 2.5 years after planting). Values within a column followed by the same letter do not differ significantly (LSD test; α=0.05). Statistical analyses were performed on transformed data, but actual means are shown for clarity. Legumes are ranked from greatest to least mean dry weight across all sites.

Species	Ninety Mile Beach	Muriwai Beach	Santoft Beach	All sites
Chamaecytisus palmensis (c)		1998 a		1998 a
Chamaecytisus palmensis (a)		992 a		992 a
Teline stenopetala		812 a		812 a
Chamaecytisus palmensis (b)		602 a		602 a
Acacia sophorae	602 a	245 ab	602 a	446 a
Acacia saligna	99 ab	221 ab	403 a	221 ab
Medicago arborea			200 ab	200 abc
Dorycnium hirsutum	40 bc	81 bc	245 ab	110 abc
Dorycnium rectum	33 bcd	299 ab	67 cd	99 abc
Dorycnium pentaphyllum	37 bcd	40 bc	99 bc	60 c
Lotus tenuis	2 d	40 bc	33 de	25 cd
Lathyrus latifolius	2 d	49 bc	40 cde	25 cd
Hedysarum coronarium	9 cd	49 bc		20 cd
Lotus pedunculatus	4 d	18 c	20 e	12 d
Lotus corniculatus	5 d	16 c	7 f	9 d
Astragalus cicer		0 d	3 f	2 e
Trifolium ambiguum			0 g	0 f

observed was much lower (20–40 kg/ha in *Lathyrus latifolius*, *Dorycnium rectum,* and *D. hirsutum*).

The potting mix (which contained fertiliser) would have contributed nitrogen to the trial site ecosystem at time of planting. The effect of this was likely to have been short-lived. Gadgil, Sandberg & Lowe (1999) found no significant growth differences between plants raised and transplanted with beach sand and those raised and transplanted with potting mix during the third year after planting at a North Island coastal dune site. They concluded that the growing/transplanting medium had a minor and transitory effect on the growth of nitrogen-fixing plants.

Wanjiku *et al.* (1997) conducted ^{15}N isotope dilution studies in a parallel 14-species screening trial in a sand dune forest adjacent to Muriwai Beach. In the understorey of a 4-year-old *Pinus radiata* stand, *Lathyrus latifolius, Dorycnium hirsutum,* and *Lotus pedunculatus* had shown the greatest persistence and highest rates of growth and nitrogenase activity. These three species all had high dependence on nitrogen derived from the atmosphere (81–98%), but annual nitrogen fixation rates recorded for *Lathyrus latifolius* (at least 214 kg/ha) were much higher than those for *Dorycnium hirsutum* (71 kg/ha) or *Lotus pedunculatus* (55 kg/ha). In this study, the relatively high nitrogen accumulation values recorded for *Lathyrus latifolius* plants at three, widely separated, open dune sites, and the relatively high nitrogenase activity demonstrated at two of these, provide further evidence that this species can make a substantial contribution to the nitrogen status of the sand dune ecosystem at a range of sites. Other species with high nitrogen-accumulation potential at specific sites were *Chamaecytisus palmensis* (a), *Dorycnium hirsutum*, *D. pentaphyllum*, *D. rectum*, *Lotus corniculatus*, *L. tenuis,* and *Medicago arborea*.

Contribution to Vegetation Cover

Assessment of the spread of individual plants provided information about the ground-covering capacity of each species. In the context of semi-stable dune sand, plant cover has a positive effect because it protects the sand surface from erosive wind action (Lancaster & Baas 1998; Hesp 2004) and also from the very high diurnal temperatures associated with direct insolation (Martinez 2003). Shading reduces evaporation of ground moisture and provides microsites favourable for the establishment of plant and animal species that would otherwise be excluded by the rigorous environmental conditions (Martinez & Garcia-Franco 2004). Lateral extension also increases the area of sand that will receive plant leachates and litterfall additions to the "soil" organic matter pool (Gadgil 1971a, b) and thus to the commencement of soil formation.

Planted *Spinifex sericeus* and *Ammophila arenaria* establish rapidly in unstable and semi-stable sand but are unlikely to provide complete ground cover within 2 years without very close spacing and regular treatment with nitrogenous fertiliser. This is because *S. sericeus* plants produce a few long rhizomes and *A. arenaria* plants have an upright tussocky habit. Nine of the legume species (ranked 3 or greater in Table 12) had achieved a mean spread of at least 50 cm within 2.5 years at all three sites (five more species at two sites) and were thus covering a considerable proportion of the bare sand between existing *S. sericeus* and *A. arenaria* plants.

TABLE 12–Ranking of selected attributes of evaluated species based on current trial results and other limited experience in the coastal sand dune environment. Within each column, higher numbers indicate relatively greater expression of the listed attribute.

Species	Long-term survival	Weed potential	Ground cover	Potential nitrogen input
Acacia saligna	5	2	3	3
Acacia sophorae	8	4	5	4
Astragalus cicer	3	1	1	2
Chamaecytisus palmensis	5	2	4	3
Dorycnium hirsutum	8	2	3	3
Dorycnium pentaphyllum	5	2	3	3
Dorycnium rectum	7	2	3	3
Hedysarum coronarium	4	2	2	3
Lathyrus latifolius	7	3	3	5
Lespedeza cuneata	1	1	1*	1
Lotus corniculatus	6	2	2	3
Lotus pedunculatus	7	2	3	3
Lotus tenuis	6	2	2	3
Lupinus nootkatensis	1	1	A	1
Medicago arborea	3	1	2	4
Sutherlandia frutescens	1	1	3*	A
Teline stenopetala	4	2	4	3
Trifolium ambiguum	2	1	1	1

* = One trial site only
A = Species disappeared or was not assessed

Possible Weediness

Although rapid establishment and maintenance of a continuous plant cover are essential during the management of unstable sand, species that exceed an optimum lateral growth rate have potential for becoming a nuisance. They are unlikely to be easily confined to the area in which they have been planted and will be regarded as weeds if they are perceived to be a threat to land management in adjacent sites. They will also be regarded as weeds if they suppress other species considered to make a useful contribution to ecosystem development. The definition of an optimum lateral growth rate will depend on many, mainly local, factors. The ability of individual plants to extend horizontally for more than 1 m within 2.5 years would certainly suggest potential for suppression of other species if practicable control measures were not available. Rapid extension growth in a wide range of sand dune conditions could imply potential for unwanted spread in sheltered areas.

Species that extended more than 1 m within 2.5 years at two or three sites were *Acacia sophorae, Chamaecytisus palmensis (a)*, *C. palmensis* (c), and *Dorycnium hirsutum*, all woody shrubs. The fact that *Acacia* and *Chamaecytisus* spp. had also attained a height of over 1 m during this time justified a request from land managers for their removal from the trials. Since *D. hirsutum* is a low-growing shrub (maximum recorded height over 4.5 yr = 74 cm) it was not perceived to be a potential threat to forestry operations.

Possible Usefulness as Nurse Species

The effectiveness of the *Ammophila arenaria*/*Lupinus arboreus* combination in protecting young *Pinus radiata* plants on open sand dunes has been demonstrated unequivocally (Restall 1964; Wendelken 1974). It provides a useful basis for suggesting that other sand-binding grasses and legumes could be used to shelter and improve the nutritional status of other later successional species. Many members of intermediate and climax communities on sand dunes are not able to colonise bare sand. Like *P. radiata*, they may succeed if they are protected and nourished during the establishment phase.

In a managed ecosystem, the ideal nurse species would be one that develops rapidly but is eventually suppressed by a more desirable plant community. In twentieth century sand dune forestry, *A. arenaria* was an ideal nurse for *L. arboreus*, but *L. arboreus*, although tolerant of a very wide range of site conditions, was not an ideal nurse for *P. radiata*. Forest managers were often frustrated by the size and woody nature of the plants which necessitated expensive releasing procedures and often made access to tree stands difficult. Experience has proved that reliance on a single species is unwise (Gadgil, Douglas, Sandberg, Lowe & Foote 1999).

Several of the species examined in this study have potential for increasing vegetation cover on sand dunes and some of them may be more suitable than *L. arboreus* for use as nurses for later successional species. Careful consideration of their attributes in relation to local conditions and to the components of the final plant community will be essential, and only the broadest of recommendations can be attempted here. Species unlikely to survive in the area just behind the current foredune are *Lespedeza cuneata*, *Lupinus nootkatensis*, *Sutherlandia frutescens,* and *Trifolium ambiguum. Acacia* spp. and *Chamaecytisus palmensis* may be useful for urgent sand stabilisation in small, isolated areas where there is no danger of spread into adjacent property. Of the remaining 11 species, *Lathyrus latifolius* is likely to contribute the most nitrogen to the ecosystem, but its persistence and scrambling habit make it less acceptable as a nurse. As indicated in Table 12, the three *Dorycnium* and three *Lotus* species, with *Astragalus cicer, Hedysarum coronarium, Medicago arborea,* and *Teline stenopetala* all possess attributes that could contribute to the development of a continuous vegetation cover in the area just behind the current foredune.

CONCLUSIONS

The planting of leguminous plant species on sand dunes for the purpose of increasing the vegetation cover is likely to be acceptable if there is a perception that they will remain confined to the planted area and will act as temporary nurses for later successional species, rather than competitors. Legumes with attributes similar or superior to those once considered desirable in *Lupinus arboreus* for this purpose are *Dorycnium hirsutum, D. pentaphyllum, D. rectum, Lathyrus latifolius, Lotus corniculatus, L. pedunculatus,* and *L. tenuis.* Of these, *Lathyrus latifolius* would probably be rejected because of its weed potential (ranked 3, Table 12) arising from its scrambling habit. On the basis of specific criteria some of the other species studied may be more acceptable at specific sites. The use of mixtures, rather than reliance on a single species, is recommended.

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