

An experimental investigation into the response of New Zealand sand dune species to different depths of burial by sand

M. T. SYKES¹ and J. B. WILSON

Department of Botany, University of Otago, Dunedin, New Zealand

SUMMARY

Thirty species found on New Zealand sand dunes were used in an experiment to investigate plant responses to burial. Plants were grown in four different treatments: surface (no burial), burial to two-thirds plant height, fully buried and full burial plus a further third of plant height, for 15 weeks. Over half the species were little affected in their biomass until fully buried. Shoot:root ratios usually decreased with burial depth, though six species showed increases. In *Ammophila arenaria*, the common dune builder, tillering occurred after partial burial but plant biomass was much lower than in surface plants. Full burial usually killed the plant, though some were still alive at the lowest depth. The ability to stay alive in mobile dunes is important. Of the other grasses examined, many perennial species survived partial burial, though full sand cover killed most. Many annual grasses, e.g. *Bromus diandrus* and *Lagurus ovatus*, were intolerant of even partial burial. The plastic nature of the morphological development of many species was emphasized. This was quantified to some extent for some species using leaf:stem ratios. Two species, *A. arenaria* and *Desmoschoenus spiralis*, had decreased ratios as the stem elongated in response to burial. The ratio increased, however, in *Hydrocotyle novae-zelandiae* as the petiole lengthened. Morphological effects were varied; creeping herbs responded well to burial, with some, e.g. *Centella uniflora* growing up to the surface from fully plus a third buried. Burial often produced elongation of stems, e.g. in *Lupinus arboreus* and *Euphorbia glauca*. In *Phormium tenax* new leaves growing buried by the sand were a crinkled zig-zag shape. Correlations between burial response and field positions from four sand dune systems in southern New Zealand were mostly non-significant. However, at Cole Creek on the West Coast, positive partial burial responses were significantly negatively correlated to distance from the sea. Tolerance of sand deposition appears to be as necessary for rear dune species as it is for those of the front dunes.

Key-words: dunes, morphological responses, New Zealand, *Ammophila arenaria*, sand burial.

¹Present and corresponding address: Dr M. T. Sykes, Institute of Ecological Botany, University of Uppsala, Box 559, S-751 22 Uppsala, Sweden

INTRODUCTION

Ability to survive sand burial is of primary importance to dune species (Nobuhara 1967; van der Valk 1974). Stabilization of sand is achieved by vegetation accumulating sand and growing up through it. In Europe, this role is often performed by *Ammophila arenaria*; in southern New Zealand by *Desmoschoenus spiralis* (Cyperaceae), though *A. arenaria* has been introduced. Moreover, dune species must be able to cope with sand destabilized by occasional and severe environmental events, such as a particularly high tide or a blowout. Even small forbs which never actively form dunes are subject to such deposition of sand, and must grow up to the surface to survive.

Previous work has mainly examined germination and/or seedling response to burial (van der Valk 1974; Maun & Riach 1981; Lee & Ignaciuk 1985; Maun & Lapierre 1986; Harris & Davy 1987, 1988). The ability to survive sand burial is a continuing problem for most dune species, so response in mature plants is also important. Only a few species have the ability to survive sand accretion and have been examined experimentally (Moreno-Casasola 1986), notably *A. arenaria* and *A. breviligulata* (Ranwell 1958; Disraeli 1984). There has been no previous survey of the burial tolerance of a dune flora.

In this study, established plants of 30 native and exotic species of New Zealand dunes were experimentally buried at different depths. Responses of each species to burial were measured by observing whether such species could survive long periods of burial and also whether, if fully buried, they could subsequently reach the surface. Since ability to survive burial was likely to be related to plant height, species were buried to a particular proportion of their height.

MATERIALS AND METHODS

Species were either collected from the field or germinated from seed. For the experiment, plants were grown in a John Innes-type potting compost, with general fertilizer (6N:5P:5K at 3.1 g l⁻¹) and calcium carbonate (0.6 g l⁻¹), each plant in a 120-mm diameter plastic pot. The pots were grown under glasshouse lights. These general soil, nutrient and lighting conditions were selected to give uniformity for all species and treatments. Field experiments were not carried out at this time because of the inaccessibility of undisturbed dune sample sites. Further, field experiments may well be prone to extraneous events which make it difficult to isolate the variable being examined. They are, however, in principle, a useful addition to a glasshouse study of this type.

Two months after being placed under lights, similarly sized plants of each species were selected for the experiment. The pot in which the plants were growing was placed on a layer of gravel within a larger pot which was itself enclosed in a plastic bag to prevent leaking after watering. This combination pot was then buried at the selected depth in a randomly specified position within large wooden boxes. To prevent slumping, each pot was set on a block of wood. The plants were held gently upwards as if they were blown by wind, as the sand was filled in around them. Each wooden box was treated as a randomized block and was replicated twice.

There were four burial treatments, related to the height of each species (H): 0.0 H (surface, no burial), 0.66 H (two-thirds burial), 1.0 H (full burial) and 1.33 H (burial to the

plant's height, plus one-third). H was defined as the height of the individual plant as buried.

Each pot was watered weekly with 200 ml of quarter-strength nutrient solution (Hewitt 1966) to reduce the possibility of nutrient deprivation affecting burial responses. This solution was applied via a rubber tube which ran from the surface of the sand to underneath the inner pot. The surface of the sand was watered as it dried out, normally every second or third day. The sand below the surface remained moist but not waterlogged throughout.

The glasshouse was lit for 12 h per day by mercury vapour lights, each of 400 watts, at one light m^{-2} , which gave an extra $32 W m^{-2}$ light intensity at the sand surface. There was no additional heating. Air vents opened when temperatures exceeded $15^{\circ}C$. The mean temperature during the experiment was $16.6^{\circ}C$ and mean relative humidity 78.6%. Sand temperature on a typical day decreased with depth: $25^{\circ}C$ on the surface under lights, $16^{\circ}C$ at 150 mm depth, and $12^{\circ}C$ at 700 mm.

After 15 weeks in the boxes, plants were carefully removed and compost washed from the roots. Plants were divided into root, shoot (including buried stem) and dead material, dried at $95^{\circ}C$ for 48 h and weighed.

Nomenclature follows Allan (1961) for native dicotyledons, Moore & Edgar (1970) for native monocotyledons except Cheeseman (1925) for native Poaceae; changes reported by Connor & Edgar (1987) were included, and Clapham *et al.* (1981) were followed for adventive species except where indicated.

RESULTS

Total plant biomass

Species differed significantly in their response to burial (Table 1). Only 25% of the 30 species were significantly reduced in biomass by 0.66 H burial, e.g. *Bromus diandrus*. Most other species were significantly reduced by full (1.0 H) burial, e.g. *Acaena anserinifolia*. Others were either not affected until 1.33 H burial, e.g. *Gnaphalium luteo-album*, or were relatively little affected by any degree of sand burial tried, e.g. *Phormium tenax*. In a few species dry weight increased, significantly in *Lupinus arboreus*.

Partitioning of biomass and morphology

The response of shoot:root ratio differed significantly between species (Table 2). In most species it decreased with burial, but for four species at 0.66 H burial it increased, e.g. in *Desmoschoenus spiralis*. Only one species (*Euphorbia glauca*) had an increase in the full burial treatment while *Hydrocotyle novae-zelandiae* was the only species where the ratio increased up to the burial depth of 1.33 H .

The ratio of live leaf:stem weight responded differently between species (Table 3). Two species, *A. arenaria* and *D. spiralis*, had a lower leaf:stem ratio with partial burial, while *H. novae-zelandiae* had a higher ratio.

The morphology of some species was affected by partial burial (Fig. 1). In some species, e.g. *A. arenaria*, *Carex pumila*, plants responded to the stimulation of partial sand burial by producing adventitious roots above pot soil level (Fig. 1b,d and h). The partially buried original shoot material in some species died off and is therefore not shown (Fig. 1d).

Table 1. Total plant dry weight (g) at final harvest of 30 species not buried (surface) or buried to various proportions of their height (H)

Species		Burial depth			
		Surface	0.66 H	1.0 H	1.33 H
<i>Acaena anserinifolia</i>	E	9.77 a	11.41 a	0.03 b	0.40 c
<i>Ammophila arenaria</i>	I	8.65 a	1.15 b	0.31 b	0.32 b
<i>Austrofestuca littoralis</i>	N	3.73 a	1.39 a	0.51 b	0.52 b
<i>Bromus diandrus</i>	I	12.78 a	0.55 b	0.22 b	0.28 b
<i>Carex pumila</i>	N	14.81 a	5.35 a	0.59 b	1.10 b
<i>Centella uniflora</i>	E	5.51 a	4.64 a	2.04 a	0.22 b
<i>Colobanthus muelleri</i>	E	0.31 a	0.11 a	<0.01 b	<0.01 b
<i>Coprosma acerosa</i>	E	7.57 a	5.44 a	0.02 b	0.02 b
<i>Craspedia uniflora</i>	E	14.20 a	9.36 a	0.53 b	0.02 c
<i>Cyperus ustulatus</i>	E	49.63 a	35.47 a	2.46 b	5.81 b
<i>Desmoschoenus spiralis</i>	E	19.73 a	8.46 a	6.10 a	6.30 a
<i>Elymus farctus</i>	I	29.80 a	27.72 a	0.40 b	0.82 b
<i>Euphorbia glauca</i>	E	23.73 a	16.41 a	0.38 b	0.29 b
<i>Geranium sessiliflorum</i>	E	3.52 a	0.27 b	No data	0.03 c
<i>Gnaphalium audax</i>	E	13.32 a	6.42 a	0.02 b	0.06 b
<i>G. luteo-album</i>	N	28.52 a	27.89 a	18.37 a	0.04 b
<i>Gunnera albocarpa</i>	E	1.04 a	0.06 b	0.09 b	0.08 b
<i>Holcus lanatus</i>	I	39.32 a	52.80 a	0.22 b	0.11 b
<i>Hydrocotyle novae-zelandiae</i>	E	6.90 a	3.43 a	No data	0.08 b
<i>Lachnagrostis lyallii</i>	N	10.11 a	3.01 a	0.23 b	0.32 b
<i>Lagenifera pumila</i>	E	7.92 a	8.32 a	0.47 b	0.01 c
<i>Lagurus ovatus</i>	I	20.61 a	7.89 a	0.15 b	0.09 b
<i>Lupinus arboreus</i>	I	23.13 a	116.43 b	2.55 c	0.04 d
<i>Phormium tenax</i>	E	4.24 a	4.25 a	1.49 a	2.32 a
<i>Plantago triandra</i>	E	3.37 a	4.05 a	2.52 a	0.12 b
<i>Poa pusilla</i>	E	17.27 a	2.28 b	0.23 c	0.40 c
<i>Scirpoides nodosa</i>	N	17.72 a	4.12 a	0.74 b	1.29 b
<i>Senecio elegans</i>	I	17.43 a	78.51 b	1.63 a	0.03 c
<i>Silene gallica</i>	I	88.94 a	109.83 a	6.44 b	0.21 c
<i>Wahlenbergia congesta</i>	E	1.36 a	0.06 b	0.01 b	0.02 b

Within species, depths with the same letter are not significantly different ($P \geq 0.05$, data log-transformed). The status of the species is indicated by the code, I = introduced; N = native; E = endemic to New Zealand. For statistical effects: Sp = species; Bu = burial treatment. Significant effects ($P < 0.05$): Sp, Bu, Sp \times Bu. Error MS: 1.0141810 (222 d.f.).

Correlation with field position

Species scores from the first vegetation gradient (axis) given by ordination plotted against the ratio of live plant dry weights from 1.0 H burial to that of 0.0 H (surface) gave no significant correlations. Ordination scores plotted against the ratio of live plant dry weights from 0.66 H burial to that of surface-grown plants gave a significant correlation at Cole Creek (Fig. 2), tolerance to partial burial being negatively associated with closeness to the sea ($r = 0.514$, $P < 0.05$). Such correlations at the other sites were similar but non-significant.

Table 2. The ratio of shoot:root weight at final harvest of 30 species not buried (surface) or buried to various proportions of their height (H)

Species		Burial depth			
		Surface	0.66 H	1.0 H	1.33 H
<i>Acaena anserinifolia</i>	E	2.61 a	3.18 a	0.10 b	0.29 b
<i>Ammophila arenaria</i>	I	3.88 a	3.95 a	2.21 a	2.95 a
<i>Austrofestuca littoralis</i>	N	3.02 a	4.66 a	0.01 b	3.06 a
<i>Bromus diandrus</i>	I	1.82 a	0.31 b	0.10 b	0.15 b
<i>Carex pumila</i>	N	1.92 a	5.56 a	0.19 b	0.16 b
<i>Centella uniflora</i>	E	6.27 a	7.41 a	6.17 a	0.81 b
<i>Colobanthus muelleri</i>	E	6.89 a	1.63 b	0.10 c	0.10 c
<i>Coprosma acerosa</i>	E	7.76 a	13.08 a	0.10 b	0.10 b
<i>Craspedia uniflora</i>	E	2.19 a	2.15 a	0.92 a	0.10 b
<i>Cyperus ustulatus</i>	E	1.64 a	2.30 a	1.47 a	2.62 a
<i>Desmoschoenus spiralis</i>	E	18.68 a	119.98 b	41.70 ab	22.15 a
<i>Elymus farctus</i>	I	1.77 a	8.73 b	0.10 c	0.10 c
<i>Euphorbia glauca</i>	E	2.72 a	3.75 a	19.44 b	3.21 a
<i>Geranium sessiliflorum</i>	E	No root in some treatments			
<i>Gnaphalium audax</i>	E	2.26 a	3.25 a	0.10 b	0.50 c
<i>G. luteo-album</i>	N	7.75 a	9.58 a	12.21 a	0.09 b
<i>Gunnera albocarpa</i>	E	0.91 a	0.10 b	0.10 b	0.10 b
<i>Holcus lanatus</i>	I	0.43 a	1.30 a	0.10 b	0.10 b
<i>Hydrocotyle novae-zelandiae</i>	E	2.57 a	5.14 ab	No data	12.87 b
<i>Lachnagrostis lyallii</i>	N	2.71 a	0.75 b	0.10 b	0.10 b
<i>Lagenifera pumila</i>	E	1.30 a	0.61 a	0.84 a	0.10 b
<i>Lagurus ovatus</i>	I	3.01 a	3.82 a	0.10 b	0.10 b
<i>Lupinus arboreus</i>	I	2.98 a	8.26 a	9.93 a	0.10 b
<i>Phormium tenax</i>	E	3.24 a	4.95 a	2.76 a	3.18 a
<i>Plantago triandra</i>	E	3.07 a	4.14 a	4.61 a	0.10 b
<i>Poa pusilla</i>	E	0.41 a	2.41 b	0.10 c	0.10 c
<i>Scirpoides nodosa</i>	N	5.44 ab	15.87 a	2.73 b	2.73 a
<i>Senecio elegans</i>	I	3.39 a	13.39 b	3.42 a	0.10 c
<i>Silene gallica</i>	I	58.49 a	56.70 a	7.47 b	3.10 b
<i>Wahlenbergia congesta</i>	E	7.07 a	0.65 b	0.09 c	0.82 b

See Table 1 for abbreviations.

Significant effects ($P < 0.05$): Sp, Bu, Sp \times Bu.

Error MS: 0.6268185 (212 d.f.).

DISCUSSION

Antos & Zobel (1985) noted a range of plastic responses to volcanic tephra burial. In this study a similar range of responses to sand burial was seen. Most species buried under volcanic tephra took a vertical line to the surface as did the creeping species here. In contrast, rhizomes produced by *E. glauca* when partially buried, grew horizontally for some distance (Fig. 1f).

In *A. arenaria* (Fig. 1c and d) and *D. spiralis* there was a decrease in leaf:stem ratio on partial burial. In *A. arenaria* this was reflected in the extension of the stem internodes producing substantially taller (900–1200 mm) plants than in surface treatments

Table 3. The ratio of live leaf to live stem at final harvest of those species for which information is available, grown on the sand surface and partially buried (0.66 H)

Species		Burial depth		P-value
		Surface	0.66 H	
<i>Ammophila arenaria</i>	I	32.14	3.42	<0.001
<i>Austrofestuca littoralis</i>	N	8.20	3.93	0.095
<i>Centella uniflora</i>	E	0.55	1.21	0.075
<i>Cyperus ustulatus</i>	E	3.45	1.21	0.186
<i>Desmoschoenus spiralis</i>	E	5.04	1.67	<u>0.013</u>
<i>Euphorbia glauca</i>	E	0.76	0.82	0.857
<i>Geranium sessiliflorum</i>	E	2.46	2.91	0.701
<i>Gnaphalium audax</i>	E	3.77	2.54	0.365
<i>Hydrocotyle novae-zelandiae</i>	E	0.17	0.48	<u>0.021</u>
<i>Phormium tenax</i>	E	31.13	32.12	0.942
<i>Plantago triandra</i>	E	2.64	4.77	0.177
<i>Scirpoides nodosa</i>	N	11.42	11.04	0.937
<i>Wahlenbergia congesta</i>	E	4.07	2.94	0.455

See Table 1 for abbreviations.

Probabilities less than 0.05 are underlined.

Significant effects ($P < 0.05$): Sp, Sp \times Bu.

Error MS: 0.327140964 (41 d.f.).

(650–800 mm). In some herbs, however, e.g. *C. uniflora*, *H. novae-zelandiae* and *G. sessiliflorum* (Fig. 1k,l), the ratio increased, and often the petiole elongated.

E. farctus responded to burial in a similar way to *A. arenaria*, with internode elongation, tiller production and adventitious rooting just below the sand surface. Plant dry weight was the same with 0.0 H and 0.66 H burial, indicating greater tolerance to partial burial than *A. arenaria*, but *E. farctus* always died when fully buried. It is typically found closer to the sea, where sand is mobile but depth of deposition less, the greater salt tolerance of *E. farctus* (Sykes & Wilson 1988; 1989) may also be a factor.

Creeping herbs such as *C. uniflora* and *H. novae-zelandiae* were generally tolerant of burial, growing to the surface from 1.33 H burial. Most of the original plant died but it was able to survive by regrowth from small pieces of stolon. In *H. novae-zelandiae* there was a substantial decrease in total dry weight with much of original material being lost (Table 1). However, the surface was reached via fine petiole extension of one or two new leaves as well as slender adventitious rooting from the remaining stolon. This was reflected in the increased shoot:root ratio at the lowest depth (Table 2). It is such a regrowth from a 'bank' (Noble *et al.* 1979) of dormant buds that is likely to be important in situations of complete burial.

In *G. sessiliflorum*, though some plants in 0.66 H burial died, there was elongation of petioles in those plants that survived (Fig. 1k,l) producing a low mound in the sand. *C. pumila* responded to partial burial by elongating rhizomes and by adventitious rooting

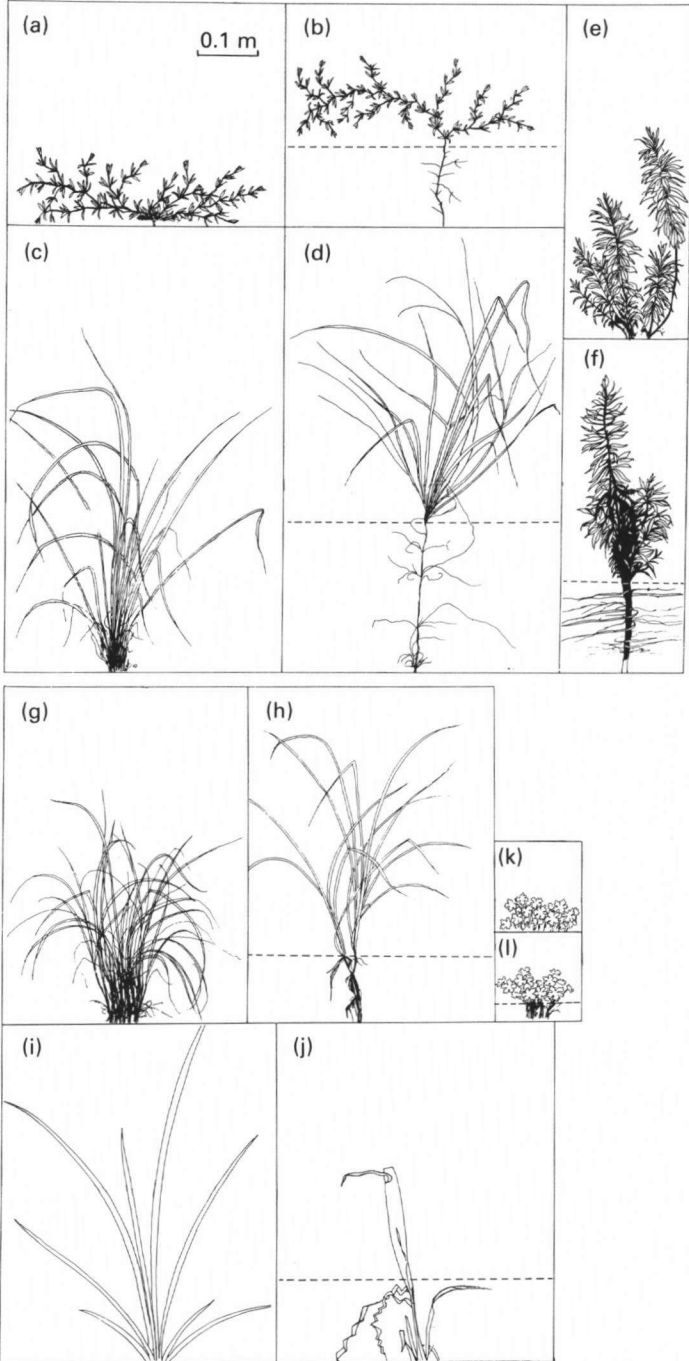


Fig. 1. Six species at harvest (drawn from photographs). All to the same scale (see a). (a,c,e,g,i,k) Surface plants; (b,d,f,h,j,l) partially (0-66 H) buried. (a,b) *Coprosma acerosa*; (c,d) *Ammophila arenaria*; (e,f) *Euphorbia glauca*; (g,h) *Carex pumula*; (i,j) *Phormium tenax*; (k,l) *Geranium sessiliflorum*. The top of the container for each plant is the base line of each drawing. The dotted line indicates the level of the sand surface for buried plants. The distance therefore between the bottom of each drawing of partially buried plants and the dotted line is the part of the plant which was completely buried.

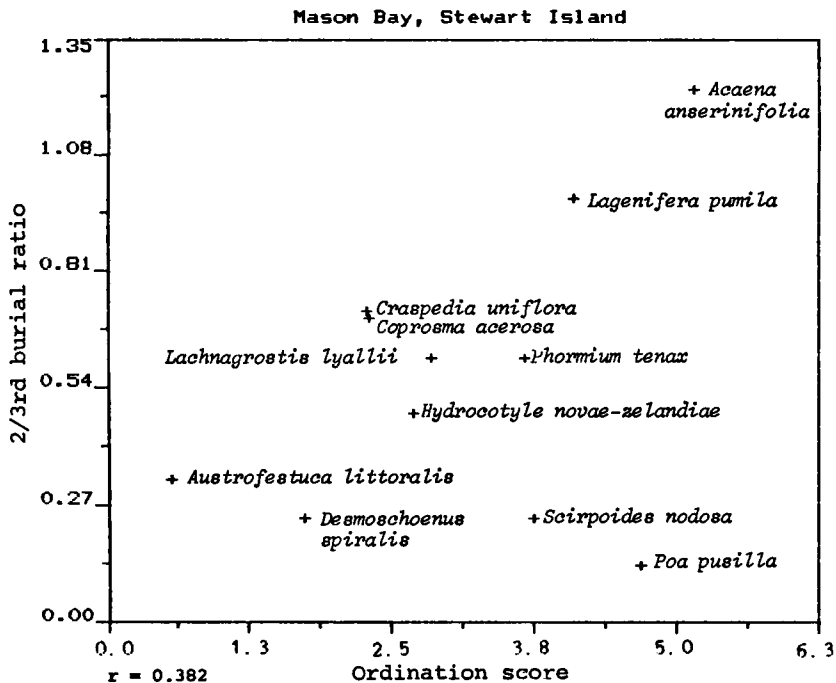
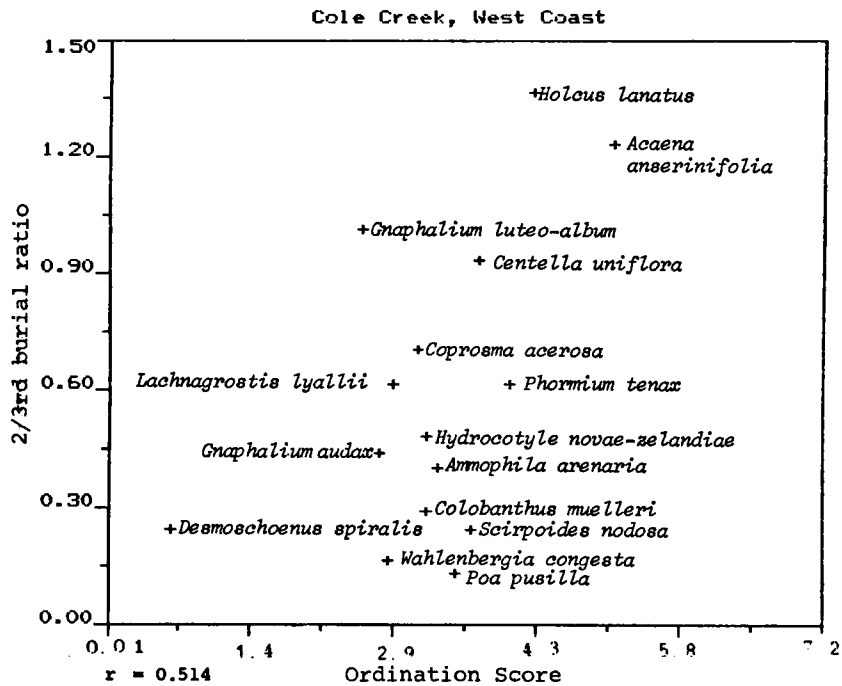
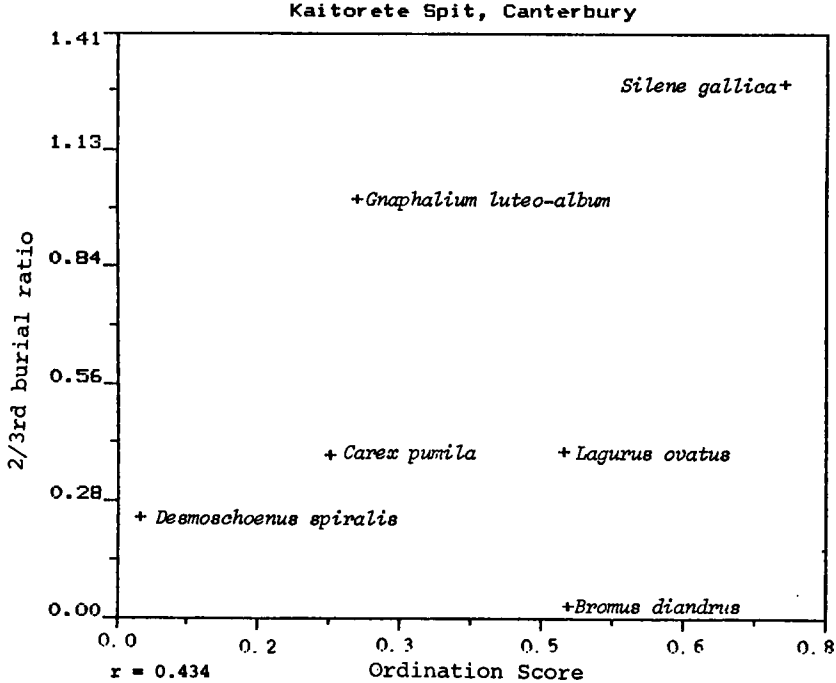
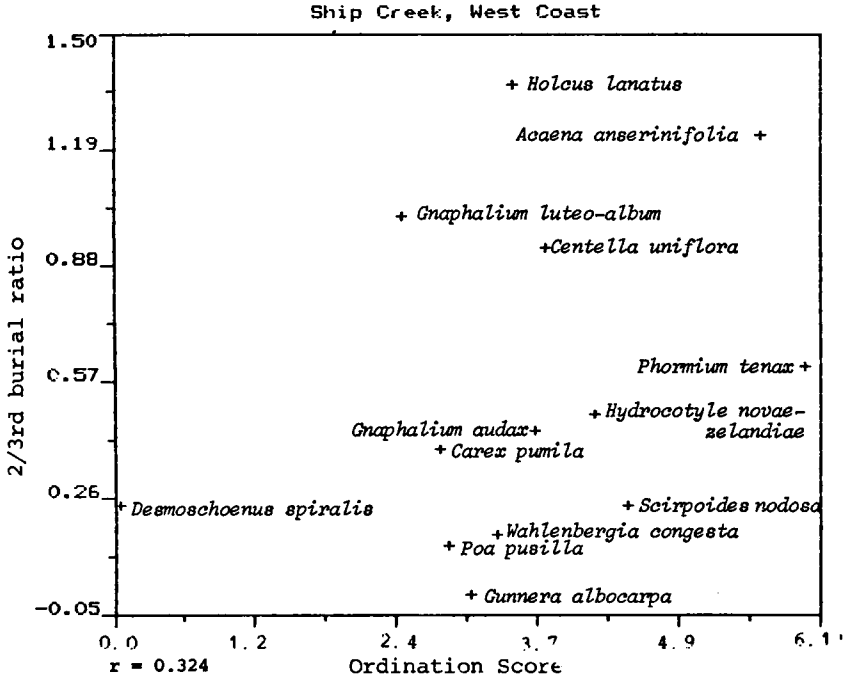


Fig. 2. Plots of the ratio of live plant dry weights from two-thirds burial: surface grown plants, against ordination scores from four dune systems in southern New Zealand. Only those experimental species recorded at each of the four sites are used in each plot.



(Fig. 1g and h), though biomass was lower (Table 1). A little live material was recorded at both 1.0 H and 1.3 H but was not considered to be new growth.

Amongst species that survived 1.0 H burial but died at 1.33 H, *G. luteo-album* responded to burial by stem elongation and rooting from nodes. *L. arboreus* responded by branching vigorously above the sand surface, 400 mm above the buried pot. *P. triandra*, normally a flat rosette, produced vertical leaves when buried. Once on the surface the leaves bent to the horizontal.

The physical effect of sand was obvious on *P. tenax* (Fig. 1i and j), new leaves from 0.66 H burial being crinkled. Such responses might be affected by the textural structure of the sand (cf. Murphy & Army 1939). At deeper burial depths there was no new growth, though the plant remained green and firm throughout the experiment. Harris & Davy (1987) reported that in *Elymus farctus* seedlings photosynthetic tissues were maintained for short periods at the expense of other organs and suggest that this is achieved by the reversal of 'the normal source-sink relationship for carbohydrate' (Harris & Davy 1988). Fully buried mature plants of *E. farctus* all died in our experiment. It is not known if the *P. tenax* plants would be able to recover sufficiently from 15 weeks of burial to resume active growth. Though as Harris & Davy (1988) point out, a passive maintenance response may well be important for survival in a disturbed habitat.

Germination and seedling emergence in dunes has been considered by others (e.g. Harty & McDonald 1972, Huiskes 1977, Watkinson 1978). Many of the species in this study reproduce vegetatively more often than by seed. Whether there is a difference between young seedlings and more mature plants in their response to burial is not known for all species, though *A. arenaria* (Ranwell 1972) and *Desmoschoenus spiralis* (personal observation) seedlings establish in moister more stable areas.

Most species used in this experiment were recorded from one or more of four native dune systems in southern New Zealand sampled for vegetation patterns. In these studies the first axis given by ordination could be interpreted as distance from the elevation above the sea. Sand movement can be related to wind exposure and is therefore likely to be greater nearer the sea. Negative correlation between burial tolerance and field position (influence of the sea) at Cole Creek emphasizes that species such as *A. anserinifolia*, *C. uniflora* and *H. lanatus* were particularly tolerant of partial burial, and were found to the rear of the dunes. At the other sites, these and similarly tolerant low herbs (e.g. *S. gallica*) were also found well away from the sea. The correlation at Cole Creek may be caused by a tendency for taller species to occur near the sea (the tolerance tested here is relative to plant height). However, the plant height versus ordination score correlation is low ($r = -0.21$) and non-significant. Although most of the species of the front dunes are tall (e.g. *D. spiralis*), other tall species are restricted to the rear dunes (e.g. *S. nodosa*). The negative correlation at Cole Creek, and lack of correlation elsewhere, therefore emphasize that burial tolerance is vital for all dune species, those of the front dunes and those of the rear, for burial is likely to occur in either situation. Although disturbances are likely to be more severe at the front of the dune they may be so severe in deposition or erosion that no survival is possible. Of course, distributions in the field are not controlled only by sand movement; Sykes & Wilson (1988) suggest that in at least some species salt spray delimits distribution.

Further experimental investigations including field studies are needed to determine the effects of periods of deposition followed by sand removal and to characterize sand regimes in the field. A complex of environmental factors affects species' distribution on dunes, of which sand burial is one.

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