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The restoration of coastal shingle vegetation: effects of substrate composition on the establishment of seedlings

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Summary

1. Shingle beach vegetation at Sizewell, Suffolk, UK, was extensively damaged by the construction of a power station. We investigated the feasibility of restoring the vegetation by directly sowing seeds of species important in the existing plant communities, in field and glasshouse experiments. The species sown were: *Crambe maritima*, *Eryngium maritimum*, *Glaucium flavum*, *Lathyrus japonicus* and *Rumex crispus*.

2. The field experiment examined the effects of proximity to the sea, composition of the beach substrate, and its amendment with organic matter on seedling emergence and establishment. There was little emergence of seedlings during the first season and most occurred in the following spring, between February and April: *G. flavum* emergence was nearly confined to this period. A low percentage of the viable seeds of all five species had emerged even after two seasons. Greatest emergence was in the monocarpic *G. flavum*, whereas the relatively long-lived perennials showed lower emergence and slower growth. Only *G. flavum* produced reproductive plants, in the second year.

3. Seedling emergence was greater in organic matter treated plots for all species and most emerged better from sandy plots than shingle dominated plots. Although *G. flavum* emergence was greater in sandy plots, seedling survivorship and growth were much greater in shingle plots; mortality showed evidence of density dependence.

4. A glasshouse experiment examined the effects of sowing density and substrate texture on the survival of *G. flavum*. On shingle, survival was negatively density-dependent, but the much lower survival on sand was density-independent. Consequently, the higher mortality on sandy field plots was probably directly associated with substrate effects.

5. Direct sowing of seeds on the beach cannot be recommended as a general technique for the restoration of shingle beach vegetation, except for annual or monocarpic species. Amendment with organic matter provided little benefit that could not have been achieved more simply by the addition of beach sand to the coarsest shingle substrates.

Key-words: beach revegetation, density-dependent mortality, *Glaucium flavum*, organic matter, soil texture.

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Introduction

Restoration of distinctive, scarce and attractive coastal plant communities after the construction of Sizewell 'B' power station (Walmsley & Davy 1997a) involved the re-establishment of key shingle beach species. In principle, the most economic approach would be to sow seeds of these species directly into the newly contoured shingle. Direct sowing, including

by hydraulic methods, has been successful in stabilizing coastal dunes, but there has been variable success in developing a mature sward (Pizzey 1975; Boorman 1977; Band 1979; Ranwell & Boar 1986). The severe environmental stresses and habitat instability result in a high risk of seedling mortality, and shingle beaches are similarly inhospitable environments for seedling establishment.

There has been no previous attempt to re-establish vegetation from seed on coastal shingle, although certain species have been sown on a small scale. Sowing

viable seeds of *Lathyrus japonicus* into 'pure shingle' resulted in virtually no germination (Brightmore & White 1963); *Crambe maritima* and *L. japonicus* sown on the shingle beach at Blakeney Point also failed to establish self-sustaining populations (White 1967). Work on *Festuca rubra* in a glasshouse showed that the fine fraction of the shingle substrate enhanced seed and water retention, seed germination, seedling establishment and drought tolerance (Fuller 1987). Similarly, in pots, seed germination and seedling growth can be significantly improved by the addition of organic tidal debris to shingle (Oliver & Salisbury 1913a). However, *in situ*, the only observations concerning germination, emergence and growth relate to naturally established seedlings. From these it appears that shingle beach vegetation development may be enhanced by the presence of organic matter (Oliver & Salisbury 1913b; Fuller 1975; Randall 1977, 1992) and organic matter or a fine substrate fraction is important for germination and establishment of *L. japonicus* and *Crambe maritima* (Brightmore & White 1963; Scott & Randall 1976).

The aim of the work described in this paper was to assess the feasibility of restoring shingle beach vegetation by sowing seed of five important and characteristic shingle beach species. The specific objectives for achieving this were: (i) to examine the effects of variations in the particle size composition of the beach substrate on seedling emergence and establishment; (ii) to determine the effect of adding organic matter to the shingle substrate on seedling establishment; and (iii) to investigate the population biology of seedling establishment.

Site description

The field experiment was carried out on the c. 50-m wide fringing shingle beach at Sizewell, Suffolk, UK (National Grid ref.: TM 475 635). The Sizewell area is underlain by early Pleistocene Norwich Crag that has produced deep, brown, calcareous sandy soils. Recent marine deposits that overlay the Crag on the beach are composed of layers of aggregate, ranging from fine sand to coarse shingle. According to Sneddon & Randall (1993), the beach substrate at Sizewell is at the sandy extreme of shingle substrates. However, the material is very heterogeneous, with some areas predominantly coarse shingle.

The vegetation on the shingle beach at Sizewell is dominated by a few clonal perennials, particularly *Honckenya peploides**, *L. japonicus* and *Ammophila arenaria*. *Rumex crispus* is a widespread and distinctive component of the vegetation. Although the dominants are perennial, *G. flavum* and *Senecio viscosus*, both monocarpic species, are widespread and common. Other species are more locally abundant, e.g. *Beta vulgaris* ssp. *maritima*, *Calystegia soldanella*,

Ononis repens and *Carex arenaria*. At the landward edge of the shingle beach, the characteristic shingle beach species are mixed with typical dune species. In contrast, at the seaward edge the dominant shingle beach species decline and a limited number of distinct strandline species, e.g. *Cakile maritima* and *Salsola kali* are associated with *Crambe maritima*, *G. flavum* and *Senecio viscosus* to form sparse vegetation cover. Landward of the shingle is a 2–5-m high marram dune ridge of variable stability. In parts the ridge consists of loose wind-blown sand, dominated by *Ammophila arenaria*, while elsewhere the sand is fully stabilized and entirely vegetated, with *C. arenaria* predominant.

The shingle beach vegetation at Sizewell has been described according to the National Vegetation Classification (NVC) and by their own shingle classification (SC) by Sneddon & Randall (1993). The more stable shingle areas are NVC *Ammophila arenaria-Festuca rubra* semi-fixed dune community (SD7) or SC *Ammophila arenaria-Carex arenaria-Festuca rubra* community (SH59); also important is the NVC *Rumex crispus-Glaucium flavum* shingle community (SD1), or SC *Ammophila arenaria-Rumex crispus-Senecio viscosus* pioneer foreshore community (SH21). Other areas may represent a *G. flavum* dominated pioneer community (NVC SD1/SC SH22) and a *Honckenya peploides-Silene maritima* pioneer community (SD1/SH26).

Methods

FIELD EXPERIMENT

Experimental design

A field experiment designed to test the effects of position relative to the sea and the effects of amendment of the shingle with organic matter was set up between 7 and 12 May 1991 on an almost unvegetated section of the shingle beach at Sizewell, in a 15 × 15-m area, between the strandline and the landward edge. An 8 × 8 matrix of plots (each 1 × 5 m, separated by 0.5- or 1-m wide paths) was established with rows parallel to the shore, such that each row and column contained four untreated/unsown (control) plots, two untreated/sown plots and two organic matter treated/sown plots.

Seed mixture, preparation and sowing

The seed mixture contained unprepared seeds of *Crambe maritima*, *Eryngium maritimum*, *Glaucium flavum*, *Honckenya peploides*, *Lathyrus japonicus* and *Rumex crispus* ssp. *littoreus*. The seed had been collected at Sizewell in 1986 and had been dried at room temperature for 5–13 weeks, before storage in air-tight plastic containers over silica gel in darkness at 2 ± 2°C (Wells, Bell & Frost 1981). Seed stocks were c. 4–5 years old at the time of sowing. Seeds of *C. maritima*

were counted directly, but for the other species the numbers were estimated from calibrated volumes (mean numbers in 10 samples of 3.3, 5.8 or 10.2 cm³, depending on size and density for each species). Samples of the seeds were pretreated and incubated in Petri dish germination tests (Walmsley & Davy 1997a) to estimate the number of viable seeds sown per plot. The estimated total and viable seed number sown per plot, the mean seed mass and the percentage germination at 25/15 °C are shown in Table 1.

Un-sown control plots were raked level, but received no other treatment. Untreated, but seeded plots were sown by broadcasting and the seed raked in. Organic matter treated plots each received 50 L of 'Forest Bark' (ICI) composted bark, which was raked into the top 10 cm of shingle before the seed was sown and raked in.

Topography and substrate composition

The field site was surveyed on a 1-m grid, using a theodolite, to obtain topographic measurements related to Ordnance Datum (OD) on 7 May 1991, and again between 11 and 15 October 1993. A single substrate core, 100 mm in diameter and 130 mm deep (1020 cm³), was taken from the centre of each plot, before sowing or substrate treatment. The samples were air-dried in a laboratory before being hand sieved through 9.5-, 4- and 2-mm sieves. The < 2-mm separate was sampled to obtain two sub-samples of c. 100–120 g. These were sieved through 0.063-, 0.125-, 0.25-, 0.5- and 1.0-mm sieves using an Endecotts mechanical shaker for 5 min. All separates were weighed to determine their relative proportions.

Maintenance and monitoring

All seedlings of species that had not been sown were removed to minimize their potential competitive effects. Regrowth of *H. peploides* from buried rhizomes proved impossible to distinguish from seedlings

without damaging excavation. Consequently, all *H. peploides* shoots were also removed.

Seedling emergence of the five species was recorded from each plot at 2-monthly intervals between February 1992 and February 1993. Emergence during the summer and autumn of 1991 had been very limited. The few 1991 plants were readily distinguishable visually and cohorts produced at different seasons during 1992 were either visually identifiable or tagged.

Glauclium flavum seedlings that had emerged in 1991 became reproductive during 1992. The reproductive capacity of these plants was estimated by recording the maximum reproductive stem height and the number of pods per plant. The growth of *G. flavum* seedlings was monitored in the sown plots in Rows 1 (seaward) and 7. Within each plot, five 10 × 10-cm subplots were positioned by selecting five out of 25 10 × 10-cm cross-wired squares in a 25 × 25-cm quadrat. The quadrat was positioned so that subplots could be chosen to include seedling densities representative of the entire plot, and avoid seedlings of other species and the mature plants of *G. flavum* established in 1991. Each subplot was photographed in June, July, August and September 1992. Total seedling density and seedling growth were derived from 10 × 15-cm photographs. The maximum seedling diameter of the five largest seedlings surviving in September 1992 was measured from the photographs for each month and scaled using the size of the 10-cm square subplot on the photograph. Further demographic monitoring was truncated by the severe inundation of the field experiment in February 1993. After burial, the site was inspected regularly between March and December 1993 to record any seedling emergence. The topographical surveys enabled the depth of burial of the seedlings to be determined.

GLASSHOUSE EXPERIMENT WITH *G. FLAVUM*

Eighteen-month old seed of *G. flavum* was stratified at 2 ± 2 °C in sand for 23 weeks to release dormancy.

Table 1. The estimated number of seeds sown in each plot, mean seed mass (mg), and the total number of seedlings emerging between February 1992 and February 1993 in all of the sown plots of the field experiment on the shingle beach at Sizewell, Suffolk. Mean percentage seed germination in laboratory tests, after appropriate pretreatment, was used to estimate the number of viable seeds sown in each plot and the percentage of emergent seedlings relative to the initial number of viable seeds sown. Seed in laboratory tests was incubated at 25/15 °C under a 12 h light/12 h dark regime. *Crambe maritima* seeds were excised from their pericarp, *L. japonicus* seed was acid scarified (96% H₂SO₄, 45 min), and *E. maritimum* and *G. flavum* seeds were stratified at 2 °C for 15 weeks before incubation

Species	Estimated seed number plot ⁻¹ (±SE)	Mean seed mass (mg)	Total emergence: number of seedlings	Seed germination % (±SE)	Estimated number of viable seeds plot ⁻¹	Total emergence: % of viable seed sown
<i>Crambe maritima</i>	25	459	88	59 ± 6.3	15	18
<i>Eryngium maritimum</i>	122 ± 1.6	11.3	41	22 ± 4.0	27	4.7
<i>Glauclium flavum</i>	1904 ± 7.9	0.95	18 277	88 ± 2.2	1675	34
<i>Lathyrus japonicus</i>	85 ± 0.6	34.9	32	91 ± 1.8	77	1.3
<i>Rumex crispus</i>	113 ± 2.5	23.2	341	100 ± 0	113	9.5

The seed was washed to remove the sand and sown in 9-cm square plastic pots containing either 100% washed horticultural sand (No. 21, Arnold Sands, Leighton Buzzard, Bedfordshire) or a 1:4 mixture of sand and 5-mm grade shingle (v/v). The seed was sown on the substrate surface and covered with 2–4 mm of sand. For both substrates 10 pots were sown with five seeds each, which were thinned to one seedling per pot after germination, and five pots each were sown with 10, 25, 50 and 100 seeds per pot. All 60 pots were placed in a randomized block in a heated (*c.* 25/15 °C) and illuminated (400 W high-pressure sodium lamps, 08:00–24:00, 16-h day) glasshouse on 24 January 1993. The pots were regularly watered and fed with 'Vitafeed 301' liquid fertilizer (360 mg N l⁻¹, 120 mg K₂O l⁻¹) after 10, 12 and 18 weeks. The arrangement of the pots was re-randomized on three occasions during the experiment. Seedling emergence and survival were recorded at first three times per week and later at reduced frequency. The experiment was terminated after 22 weeks and the remaining plants in each pot were harvested, dried (70 °C for 4 days), and weighed to obtain shoot and root dry mass.

Results

FIELD EXPERIMENT

Substrate texture

There were very large differences in the particle-size composition across the beach. The proportion of < 4 mm diameter particles was much greater in the seaward half of the beach and the proportion of > 9.5 mm diameter particles increased steadily landwards (Fig. 1f). The composition of the sand and silt fraction (< 2 mm diameter particles) of the substrate was similar throughout, although there was a smaller proportion of > 0.5 mm diameter particles and a larger proportion of < 0.25 mm diameter particles in the landward half of the field experiment (results not shown).

Seedling establishment

After sowing in May 1991, few seedlings of *G. flavum* and *R. crispus* emerged during the summer and there was some further limited emergence during the autumn. No seedlings of *C. maritima*, *E. maritimum* or *L. japonicus* appeared in the sown plots during 1991. Seedling mortality during 1991 was negligible, with very few dead seedlings among the small cohorts. In February 1992, there were only 102 *G. flavum* seedlings, 16 *R. crispus* seedlings and none of the other species in the plots. The cumulative seedling emergence from the sown plots between February 1992 and February 1993 represented a low percentage of the viable seeds sown for all five species (Table 1). Although some seedlings could have emerged and died

without trace between the censuses it is unlikely that they represented more than a small percentage of the total. *Glaucium flavum* showed the greatest overall emergence (34%); this rose to 62% in the sandier plots in the seaward half of the experiment.

There was no seedling emergence in the unsown plots during 1991 and very little subsequently. There was unlikely to have been any *in situ* soil seed bank as the surface substrate had been deposited by storm tides in December 1990. A few seedlings of *G. flavum* and *R. crispus* emerged from unsown plots during 1992 (Fig. 1), and these are likely to have been the result of seed rain from populations nearby. Apart from those sown, the only species to produce significant numbers of seedlings were *Senecio viscosus* and *Atriplex glabriuscula*, and the latter was mainly found in the seaward, sandy strandline plots.

Among the seedlings that emerged in 1991, all of the *R. crispus* seedlings and 66% of the *G. flavum* seedlings were in organic matter treated plots. Overall seedling emergence tended to be greater in organic matter treated plots for all five species in the 1992 season (Fig. 1) and significantly so in *R. crispus* ($P = 0.003$) and *C. maritima* ($P < 0.001$), according to ANOVA. Subsequently, the sown/organic matter treated plots are referred to as treated plots and the sown/untreated plots are referred to as untreated plots.

In 1991, 90% of the *G. flavum* seedlings were in the seaward half of the experiment, while 10 (63%) of the 16 *R. crispus* seedlings that emerged were in plots in the landward half. The emergence of *G. flavum* seedlings in the unsown, untreated plots was much lower in the coarse substrate (cf. Fig. 1c & f). The addition of organic matter improved emergence from the shingle substrate, but reduced emergence on the sand relative to the untreated plots. This interaction between substrate composition and treatment reduced variation in emergence across the beach for the treated plots. Although the overall cumulative seedling emergence of the other four species was low, they too showed differences in emergence across the beach. The mean number of both *G. flavum* ($P < 0.001$) and *C. maritima* ($P = 0.036$) seedlings emerging per plot in the 1992 season varied significantly across the beach (significant row effects in ANOVA). *Crambe maritima*, *E. maritimum* and *L. japonicus* also showed greater emergence from the sandy seaward plots compared to the landward plots which were dominated by coarse shingle (Fig. 1a, b & d). Only *R. crispus* showed greater emergence in the landward rows, and mainly in the treated plots (Fig. 1e). These differences in emergence can also be related to the substantial differences in the composition of the substrate across the shingle beach.

The total numbers of *C. maritima*, *E. maritimum*, *L. japonicus* and *R. crispus* seedlings emerging were too low (see Table 1) to allow a detailed examination of the temporal distribution of seedling emergence and mortality between February 1992 and February

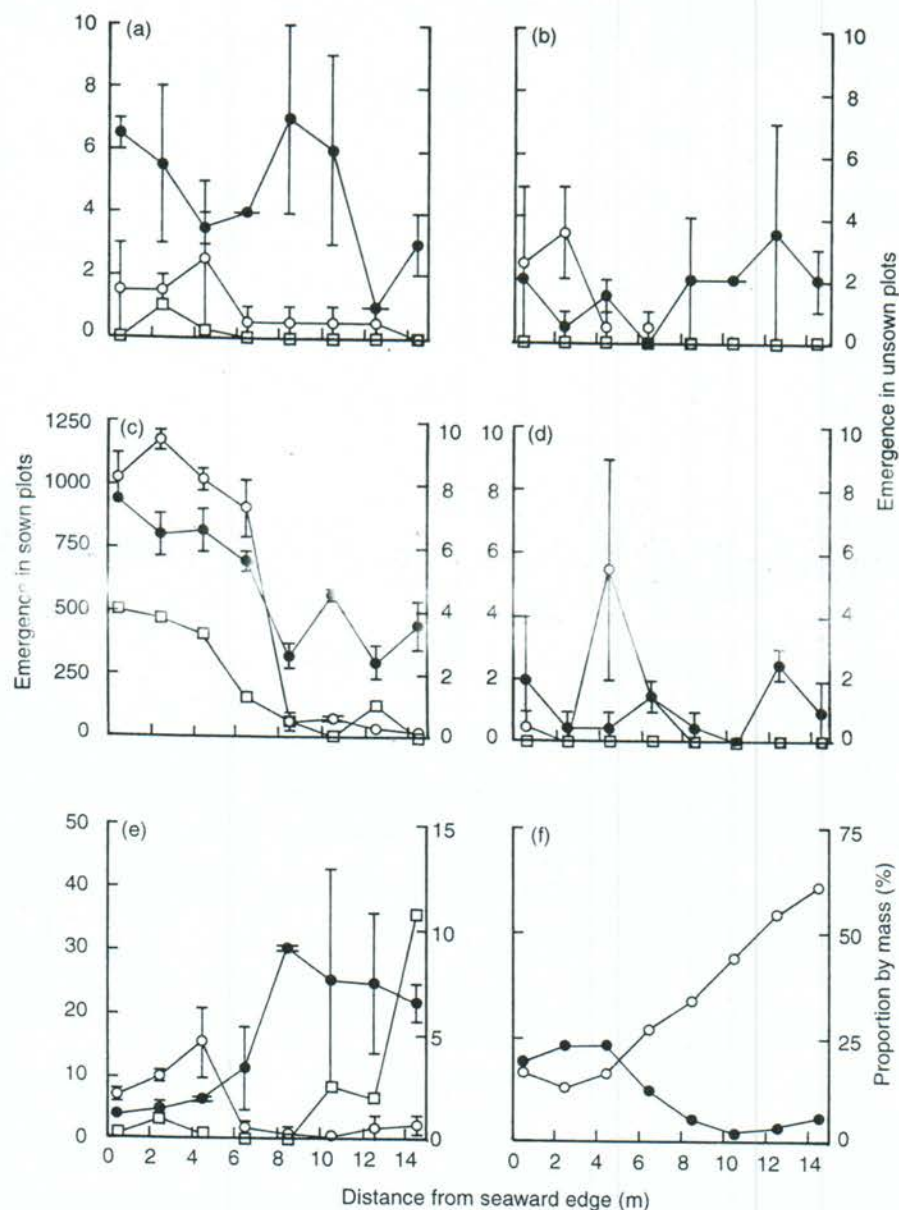


Fig. 1. Mean total cumulative seedling emergence per plot (a–e) between February 1992 and February 1993 and the proportional composition of the substrate by mass (f) across the beach at Sizewell, Suffolk, UK. The experiment ranged from seaward, sandy plots (0.5 m from the seaward edge, row 1) to landward, coarse shingle dominated plots (14.5 m from the seaward edge, row 8). Species: (a) *Crambe maritima*; (b) *Eryngium maritimum*; (c) *Glaucium flavum*; (d) *Lathyrus japonicus*; (e) *Rumex crispus*. Unsown (□, right-hand axis), sown (○, left-hand axis), and sown/organic matter treated (●, left-hand axis) plots. Substrate texture: (f) proportion of particles < 4 mm (●) and > 9.5 mm diameter (○). Error bars represent \pm SE.

1993. Almost all emergence of *C. maritima* occurred between February and April, while *E. maritimum* emergence occurred between April and June. The emergence of *L. japonicus* and *R. crispus* seedlings occurred throughout the year, although it was significantly greater in spring compared to other seasons. Seedling mortality during the summer led to a decline in the net population of *C. maritima* and *E. maritimum* seedlings, while the seedling populations of *L. japonicus* and *R. crispus* were maintained by continued emergence.

Population biology of *Glaucium flavum*

The seedling emergence, seedling mortality and net population size of *G. flavum* between February 1992

and February 1993 are shown in Fig. 2. The emergence of *G. flavum* seedlings was almost totally confined to the period February–April. There was no emergence between April and October and only six new seedlings were identified in December. A small but significant number of *G. flavum* seedlings were emerging in mid-February 1993 after the census, but this cohort was never recorded because of subsequent inundation. *Glaucium flavum* mortality was high throughout the year resulting in a rapid decline in the size of the seedling population (Fig. 2): overall survivorship was 0.08 (l_{328}) by February 1993. The pattern of *G. flavum* seedling demography for all the untreated plots was very similar to that shown by all treated plots (results not shown). Hence, the trends for all of the sown

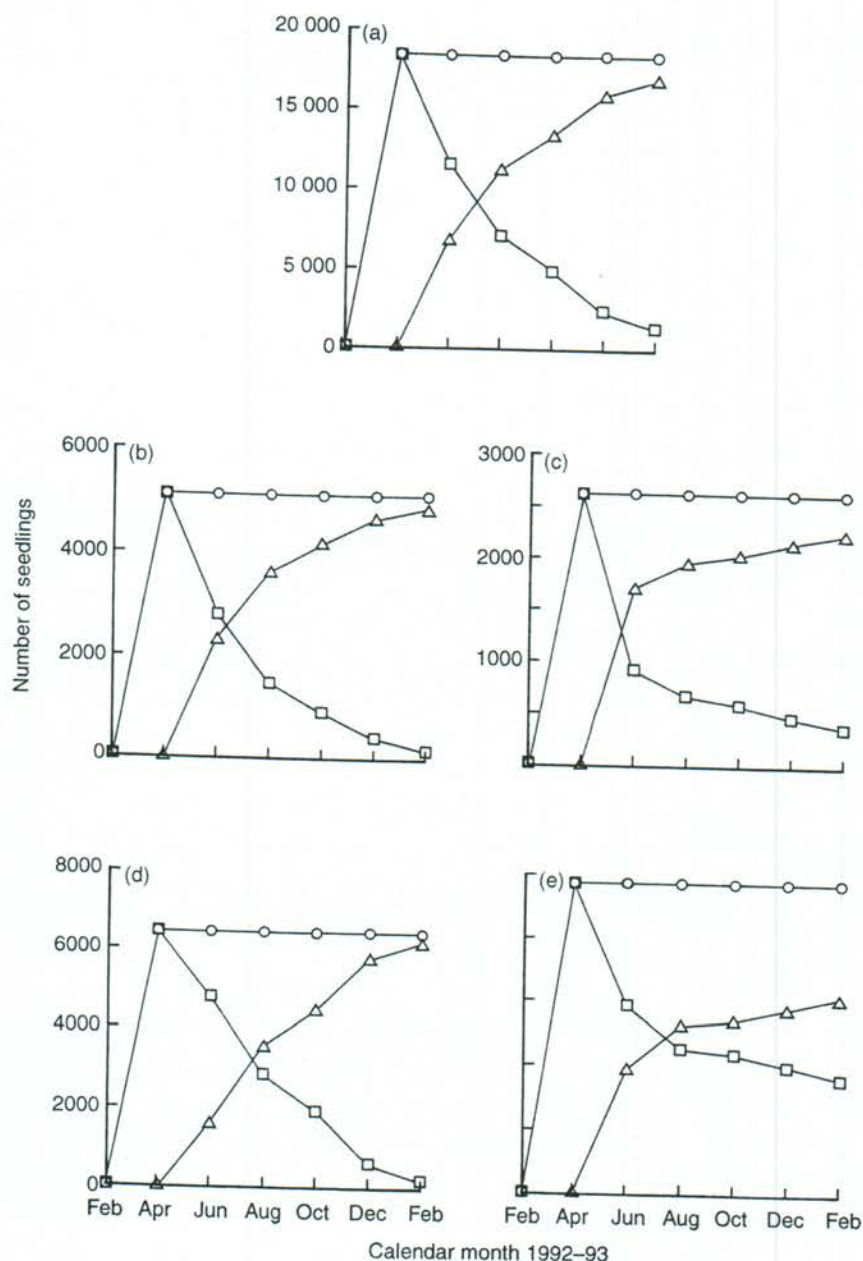


Fig. 2. Demographic changes in seedling populations of *Glaucium flavum* in the field experiment on the shingle beach at Sizewell, Suffolk: (a) all sown plots; (b) sown/organic matter treated sandy plots (rows 1-3); (c) sown/organic matter treated shingle-dominated plots (rows 6-8); (d) sown/untreated sandy plots (rows 1-3); (e) sown/untreated shingle-dominated plots (rows 6-8). Net population (\square), cumulative births (\circ) and cumulative deaths (\triangle) between February 1992 and February 1993.

plots (Fig. 2a) were extremely similar to both those in untreated and treated plots alone. However, there were differences that were related to the differences in substrate composition across the beach. In the treated sandy plots (rows 1-3), the number of deaths was greater during the summer (Fig. 2b), whereas in the untreated sandy plots, numbers of deaths were almost constant over the period (Fig. 2d). In the shingle-dominated, landward plots (rows 6-8) the number of deaths was initially greater in the treated plots (Fig. 2c) compared to the untreated ones (Fig. 2e). Without organic matter treatment, the number of deaths was also greater after August in the sandy plots (Fig. 2d)

than in the shingle-dominated ones (Fig. 2e). Although there were 5121 emergent seedlings in the seaward, sandy, treated plots and 2616 seedlings in the landward, shingle-dominated, treated plots in April 1992 (Fig. 2), differential mortality resulted in only 215 seedlings (4.2%) in the former and 370 (14.1%) in the latter by February 1993.

A negative relationship between initial seedling density in early April 1992 and the probability of survival until December (256 d later) is shown for both untreated and treated plots in Fig. 3. Sea-water, substrate inundation and salt-spray affected the probability of survival of seedlings in plots in the two most seaward

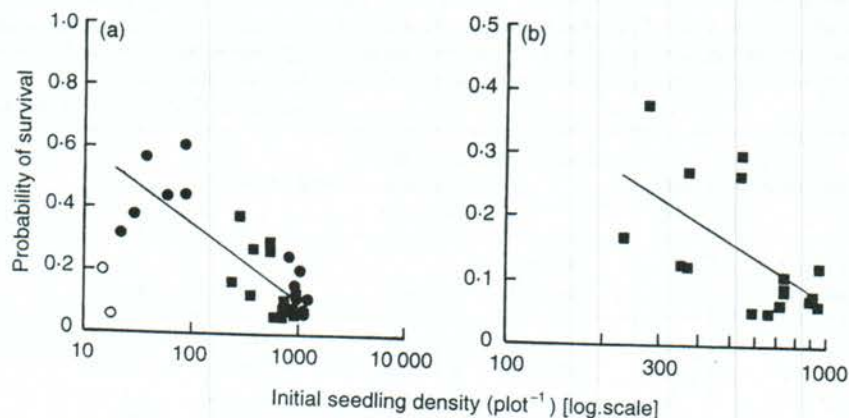


Fig. 3. The relationship between initial seedling density plot^{-1} (April 1992) and the probability of subsequent survival of *Glaucium flavum* until December 1992 in the field experiment on the shingle beach at Sizewell, Suffolk: (a) untreated (●) and treated (■) plots; (b) treated plots only (■). Density-dependent relationships are described by logarithmic regressions: (a) $y = 0.8418 - 0.1062 \ln x$ ($r^2 = 0.64$, $P < 0.001$); (b) $y = 0.991 - 0.1334 \ln x$ ($r^2 = 0.36$, $P = 0.016$). The open circles represent the most landward row of plots in which very coarse shingle (> 70% of particles > 9.5 mm diameter) resulted in very little emergence (16.5 ± 1.8 seedlings plot^{-1}) and so these points have not been included in the regression.

rows, and salt-spray also affected seedlings in other plots between January and March 1993. The significant logarithmic regression (Fig. 3a) represents data for untreated and treated plots, except for those from the untreated plots in the most landward row. These plots contained very few seedlings (16.5 ± 1.8), growing at low density in a very coarse shingle substrate (where > 70% of particles were > 9.5 mm in diameter). Adverse water relationships on this coarse shingle substrate was undoubtedly the cause of the high mortality; even coarser substrates would be expected to result in even lower seedling densities, lower survivorship and, ultimately, no germination. The relationship shown clearly cannot be extrapolated in the very coarse substrates. The effects of the organic matter treatment on seed germination apparently reduced the range of seedling density, but mortality was nevertheless density-dependent (Fig. 3b).

There was much greater growth of *G. flavum* seedlings in the predominantly shingle, landward (row 7) plots than in the seaward, sandy (row 1) plots in both untreated and treated plots (Fig. 4). Within a row, seedlings showed similar or less growth in the organic matter treated plots. None of the seedlings that emerged during 1992 became reproductive the same year, nor did the *R. crispus* seedlings that germinated in 1991. Only 42 of the 102 *G. flavum* seedlings that emerged during 1991 produced seed during 1992. Most of the reproductive plants occurred in the treated plots, where 48% of the 1991 cohort became reproductive, compared to only 28% in untreated plots (Table 2). Most of the reproductive plants were in the sandy, seaward half of the experiment, but this was merely because it contained 90% of the 1991 cohort. There were no significant differences in mean maximum flowering stem height or fecundity either between treatments or rows, although both the maximum flowering stem height and the mean number

of pods per plant were greater in organic matter treated plots (Table 2).

Effects of burial

Tidal inundation of the entire field site in February 1993 resulted in accretion of sand and shingle through-

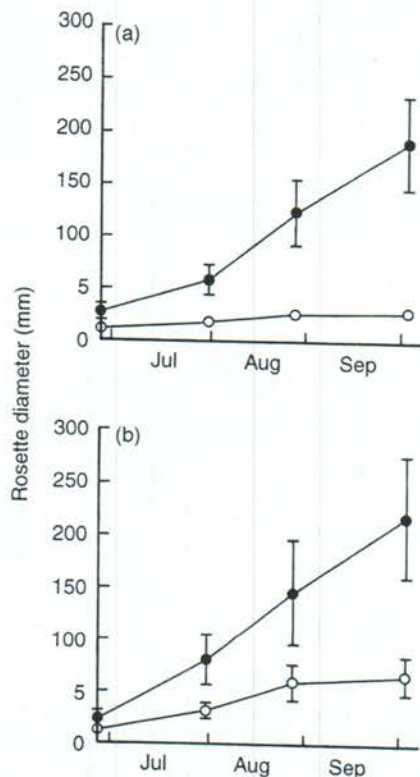


Fig. 4. The growth in mean diameter of seedlings of *Glaucium flavum* in the field experiment on the shingle beach at Sizewell, Suffolk: (a) organic matter treated plots; (b) untreated plots. The sandier, row 1 quadrats (○) are compared with the shingle-dominated, row 7 quadrats (●). Mean rosette diameter was measured from vertical, scaled photographs. The measurements were first made on 26 June and subsequently each month. Error bars represent \pm SE.

However, the probability of survival in the sand treatment is not a good linear fit therefore the slope and point of intercept cannot be determined accurately for the sand treatment. The linear regression for the *G. flavum* seedlings surviving in the sand substrate shows a gentle slope ($b = -0.002$) which is not significantly different from 0 ($P = 0.32$), indicating no significant density-dependence whereas the low intercept ($a = 0.369$) suggests that density-independent mortality is high (Fig. 5b). In contrast, plants grown in the shingle substrate showed 100% survival in pots containing a single seedling, indicating that there is little or no density-independent mortality; the poor survival at high seedling densities (Fig. 5b) resulted in a steep slope ($b = -0.012$), which is significantly different from 0 ($P = 0.001$), and indicates highly density-dependent mortality.

Seedlings grew much less in the sand substrate than in the shingle substrate at all densities; moreover, there was a density-dependent, plastic response of mass on the shingle that was not evident on the sand (Fig. 6). *Glaucium flavum* seedlings grown in shingle showed low mortality at densities up to 2500 seedlings m^{-2} (Fig. 5a) over the range of the plastic response (Fig. 6), whereas at higher densities, density-dependent mortality occurred. In contrast, the seedlings in the sand treatment showed significant mortality at all densities and little plasticity.

Discussion

SEEDLING EMERGENCE

The very low total seedling emergence for all species, except *G. flavum*, during the 20-month period that the field experiment was monitored was probably due in part to the seed dormancy mechanisms (Walmsley & Davy 1997a), which led to the creation of a long-term seed bank. Further cohorts of seedlings might have been expected in subsequent seasons had it not been

for the burial of the site. The mid-February 1993 cohort of *G. flavum* seedlings provides evidence for this. Much less emergence occurred in the coarse substrates because of the poor seed-water relationships preventing germination, and also because of the loss of seeds deep in the substrate via the large voids within coarse shingle. The burial of seeds at depth either results in seedlings germinating, but being unable to emerge, or it prevents germination as dormancy is induced because of depth-sensing mechanisms (Fenner 1985; Cordazzo 1994). A decline in seed viability in the soil seed-bank would also account for some of the failure to emerge, and may be especially important because of the aged seed used in this experiment. There was also visual evidence of seed excavation and predation in the sown plots, probably by small mammals. The large, oil-rich, highly nutritious seeds of *C. maritima* would be an obvious attraction to granivores, although seed predation has not been reported previously.

The small number of seedlings that emerged in the unsown plots shows that very little natural revegetation would have occurred in the short term in the disturbed and unvegetated shingle beach occupied by the field experiment. The numbers of naturally establishing seedlings were too small to represent a significant proportion of the seedlings in the sown plots during the study.

The greater emergence of all of the species in the field experiment on plots treated with organic matter confirmed the benefits of organic matter for seedling establishment in shingle substrates previously demonstrated in pot experiments and suggested from field observations (Oliver & Salisbury 1913a; Fuller 1975, 1987; Randall 1992). However, *G. flavum* seedling emergence was only improved by organic matter in substrates containing over 30% coarse shingle (> 9.5-mm diameter particles) and less than 10% sand (< 2.0-mm diameter particles). In contrast, emergence was reduced by organic matter in the sandy substrates (other species showed insufficient emergence to assess these interactions). Organic matter was readily incorporated into coarse substrates with low water retention capacities and large interstitial voids, thereby improving seed-water relationships and retaining seeds within the surface layers of the substrate. The addition of organic matter to predominantly sandy substrates was observed to cause the surface of the plots to dry out more rapidly rather than improving the substrate water retention capacity.

Seedling emergence across the beach profile could have been influenced by both differences in the particle-size composition of the substrate and the proximity to the sea. Clearly, in the glasshouse experiment the greater emergence in the sandy substrate could only have been a result of the substrate. In the field experiment, most species showed greater emergence in substrates with a significant fine fraction because, like organic matter, sand improves seed and water

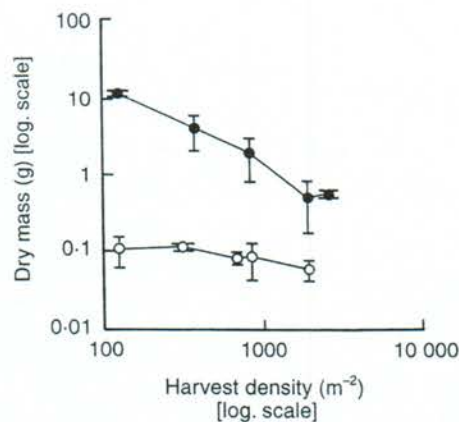


Fig. 6. The relationship between mean seedling dry mass (g) and harvest density (m^{-2}) for *Glaucium flavum* seedlings in the glasshouse experiment. Plants grown in shingle (●) and sand (○). Error bars represent \pm SE.

retention in the surface layers of the substrate and, hence, seedling emergence. Most lake shoreline plants also establish preferentially on substrates with fine particle size (Keddy & Constabel 1986). The large seeded (459 mg) *C. maritima* only suffered reduced emergence where coarse shingle formed > 50% of the substrate, whereas emergence of the small-seeded (0.95 mg) *G. flavum* was substantially affected by > 30% coarse shingle, reflecting their different probabilities of deep burial. *G. flavum* also showed a more well-defined emergence response along the gradient of substrate particle size compared to larger-seeded species, as would be expected (Keddy & Constabel 1986).

SEEDLING ESTABLISHMENT, MORTALITY AND GROWTH

Competition from neighbouring plants is often the greatest single hazard faced by colonizing seedlings (Fenner 1985), and the density-dependent mortality shown by *G. flavum* in the first year is consistent with this. However, in the physically adverse beach environment, density-independent factors can also be important (Keddy 1981, 1982), as a result of wind, tidal and wave action, salt-spray, seedling burial and erosion, sand abrasion, temperature extremes, and low moisture and nutrient availability (Maun 1994). The high mortality of *G. flavum* seedlings during the summer was clearly exacerbated by seedling desiccation and high-temperature stress. Seedlings visibly wilted and died, particularly in the bark-treated plots, which dried out rapidly near the surface. Some of this mortality was associated with necrosis at the base of the hypocotyl. This is likely to have been a result of death of phloem in the hypocotyl caused by contact with the hot substrate (Münch 1913; Levitt 1980; Maun 1994). Brief episodes of mortality in the seaward plots occurred as a result of salt-spray damage during winter storms and, in February 1993, because storm tides inundated them and deposited 1–3 cm of sand. Hence, proximity to the sea could potentially influence survival, rather than just seedling density or substrate composition.

The glasshouse experiment was designed to help resolve these confounded effects. It showed that, despite greater seedling emergence, subsequent mortality was much higher and growth substantially slower on sandy substrates than on gravel ones. Substrate *per se* was an important influence on mortality, independently of proximity to the sea. The overall density-dependent mortality suggested by the field experiment (Fig. 3) was confirmed only for shingle substrates in the glasshouse (Fig. 5). Thus, the very high mortality associated with much higher initial densities on sandy plots in the field was probably largely independent of density. The relatively low mortality in shingle-dominated plots resulted from

lower initial densities, combined with density-dependent mortality.

Once established, *G. flavum* grew well at low density on gravel-dominated substrates in the field and glasshouse, with an obvious plastic response of mass to harvest density. Its unexplained, very poor growth in the sandy plots in the field experiment and on the sand substrate treatment in the glasshouse was independent of density. *Glaucium flavum* occurs selectively on well drained, disturbed substrates (Scott 1963). The sand would have had less interstitial space and smaller voids, but aeration and drainage would have been good in both substrates by normal standards; the sand, however, was more water-retentive than the shingle. Because of their smaller size, individuals on sandy substrates would have probably been more at risk and their populations even more vulnerable to extinction (Sarukhán, Martínez-Ramos & Piñero 1984).

SHINGLE BEACH VEGETATION RESTORATION

Glaucium flavum demonstrated the ability to become established, mature and produce significant quantities of seed from a direct sowing into a suitable beach substrate. It seems likely that it could rapidly produce self-sustaining populations. Similarly sized populations were present in all plots in February 1993 regardless of their substrate composition or whether or not they had been treated with organic matter, although the plant mass varied substantially. The use of an organic matter treatment appears to have provided no benefit that could not have been achieved more simply by the addition of beach sand to the coarsest shingle substrates. Only a small proportion of fine material or organic matter is required in the substrate to achieve an adequate population of *G. flavum* seedlings.

The perennial species, which are not necessarily geared to annual recruitment, showed very poor seedling emergence and establishment after direct sowing into the shingle beach, irrespective of substrate composition or its amendment. The life histories of shingle beach species thus dictate their probability of establishment in any year. Seeding cannot be recommended as a general technique for the restoration of shingle beach vegetation because of the poor establishment of most of the species, even before burial of the entire site resulted in the death of all seedlings. Moreover, rapid, natural regeneration of the vegetation cannot be expected, as is evident from the very low emergence in unsown plots. However, the importance of totipotent roots or rhizomes in enabling establishment from vegetative fragments, especially after disturbance by storm tides, e.g. in *E. maritimum* (Turmel 1947) and *L. japonicus* (Simon 1979), suggests that seedling establishment may be relatively rare or of secondary importance. These larger inocula also have a greater capacity to emerge from burial. Such veg-

etative fragments could be used in restoration, but in practice, they would be difficult and expensive to store for long periods and would carry genetic variation that was less representative of the original population.

In the unstable shingle beach habitat it is feasible to establish annuals and short-lived monocarpic species such as *G. flavum* from seed, whereas perennials recolonize too slowly and are too susceptible to catastrophic disturbance when young. These species require more intensive methods, such as the use of container-grown plants (Walmsley & Davy 1997b).

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References

- Band, W.T. (1979) Beach management for recreation in Scotland. *Les Côtes Atlantiques de l'Europe, Evolution, Aménagement, Protection* (ed. A. Guilcher), pp. 261–268. CNEXO, Brest, France.
- Boorman, L.A. (1977) Sand dunes. *The Coastline* (ed. R.S.K. Barnes), pp. 161–197. John Wiley, London.
- Brightmore, D. & White, P.H.F. (1963) Biological flora of the British Isles. *Lathyrus japonicus* Willd. *Journal of Ecology*, **51**, 795–801.
- Cordazzo, C.V. (1994) *Comparative population studies of four dominant plants of Southern Brazilian Coastal Dunes*. PhD thesis, University of East Anglia, Norwich, UK.
- Fenner, M. (1985) *Seed Ecology*. Chapman & Hall, London.
- Fuller, R.M. (1975) The Culbin shingle bar and its vegetation. *Transactions of the Botanical Society of Edinburgh*, **42**, 293–305.
- Fuller, R.M. (1987) Vegetation establishment on shingle beaches. *Journal of Ecology*, **75**, 1077–1089.
- Keddy, P.A. (1981) Experimental demography of the sand-dune annual *Cakile edentula*, growing along an environmental gradient in Nova Scotia. *Journal of Ecology*, **69**, 615–630.
- Keddy, P.A. (1982) Population ecology on an environmental gradient: *Cakile edentula* on a sand dune. *Oecologia*, **52**, 348–355.
- Keddy, P.A. & Constabel, P. (1986) Germination of ten shoreline plants in relation to seed size, soil particle size and water level: an experimental study. *Journal of Ecology*, **74**, 133–141.
- Levitt, J. (1980) *Responses of Plants to Environmental Stresses*. Vol. 1. *Chilling, Freezing, and High Temperature Stresses*. Academic Press, London.
- Maun, M.A. (1994) Adaptations enhancing survival and establishment of seedlings on coastal dune systems. *Vegetatio*, **111**, 59–70.
- Münch, E. (1913) Hitzeschäden an Waldpflanzen. *Naturwissenschaftliche Zeitschrift fuer Forst- und Landwirtschaft*, **11**, 557–562.
- Oliver, F.W. & Salisbury, E.J. (1913a) The topography and vegetation of the National Trust Reserve known as Blakeney Point, Norfolk. *Transactions of the Norfolk and Norwich Naturalists' Society*, **9**, 485–542.
- Oliver, F.W. & Salisbury, E.J. (1913b) Vegetation and mobile ground as illustrated by *Suaeda fruticosa* on shingle. *Journal of Ecology*, **1**, 249–271.
- Pizzey, J.M. (1975) Assessment of dune stabilization at Camber, Sussex, using air photographs. *Biological Conservation*, **7**, 275–288.
- Randall, R.E. (1977) Shingle formations. *The Coastline* (ed. R.S.K. Barnes), pp. 199–213. John Wiley & Sons, London.
- Randall, R.E. (1992) The shingle vegetation of the coastline of New Zealand: Nelson Boulder Bank and Kaitorete Spit. *New Zealand Journal of Geography*, **93**, 11–19.
- Ranwell, D.S. & Boar, R. (1986) *Coastal Dune Management Guide*. Institute of Terrestrial Ecology, NERC, Huntingdon.
- Sarukhán, J., Martínez-Ramos, M. & Piñero, D. (1984) The analysis of demographic variability at the individual level and its population consequences. *Perspectives on Plant Population Ecology* (eds R. Dirzo & J. Sarukhán), pp. 83–106. Sinauer, Sunderland, Massachusetts.
- Scott, G.A.M. (1963) Biological flora of the British Isles. *Glaucium flavum* Crantz. *Journal of Ecology*, **51**, 743–753.
- Scott, G.A.M. & Randall, R.E. (1976) Biological flora of the British Isles. *Crambe maritima* L. *Journal of Ecology*, **64**, 1077–1091.
- Simon, J.-P. (1979) Adaptation and acclimation of higher plants at the enzyme level: latitudinal variations of thermal properties of NAD malate dehydrogenase in *Lathyrus japonicus* Willd. (Leguminosae). *Oecologia*, **39**, 273–287.
- Sneddon, P. & Randall, R.E. (1993) *Coastal Vegetated Shingle Structures of Great Britain*, 4 volumes. Joint Nature Conservation Committee, Peterborough.
- Stace, C.A. (1991) *New Flora of the British Isles*. Cambridge University Press, Cambridge.
- Turmel, J.-M. (1947) Multiplication végétative des *Eryngium*. II. Bouturage de l'*Eryngium maritimum* L. *Bulletin Société Botanique de France*, **94**, 138–142.
- Walmsley, C.A. & Davy, A.J. (1997a) Germination characteristics of shingle-beach species, effects of seed ageing and their implications for vegetation restoration. *Journal of Applied Ecology*, **34**, 131–142.
- Walmsley, C.A. & Davy, A.J. (1997b) The restoration of coastal shingle vegetation: effects of substrate composition on the establishment of container-grown plants. *Journal of Applied Ecology*, **34**, 154–165.
- Wells, T.C.E., Bell, S. & Frost, A. (1981) *Creating Attractive Grasslands Using Native Plant Species*. Nature Conservancy Council, Shrewsbury.
- White, D.J.B. (1967) *An Annotated List of the Flowering Plants and Ferns on Blakeney Point, Norfolk*. The National Trust, Norfolk.

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The restoration of coastal shingle vegetation: effects of substrate composition on the establishment of container-grown plants

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Summary

1. The use of container-grown plants in restoring shingle beach vegetation was investigated at Sizewell, Suffolk, UK, where the vegetation had been destroyed by the construction of a power station. Six species, *Crambe maritima*, *Eryngium maritimum*, *Glaucium flavum*, *Honckenya peploides*, *Lathyrus japonicus* and *Rumex crispus*, were selected to counter erosion and assist the development of a more complex and natural community. Plants were raised from stored seed, indigenous to the site, by horticultural techniques.
2. Shingle substrates are dry, nutrient-poor and heterogeneous in their physical composition. Field experiments investigated the efficacy of organic matter and fertilizer treatments as ameliorants, and examined the influence of position on the beach profile and substrate composition on the establishment of container-grown plants.
3. Neither organic matter nor fertilizer additions had any significant effect on mean plant size in any species after one field season. Planting location on the beach profile was the most important factor influencing establishment. *Crambe maritima*, *G. flavum*, *H. peploides* and *R. crispus* plants all grew significantly larger in the seaward plots, with more coarse shingle. Only *G. flavum* produced many reproductive plants during the first year, and these were more frequent and more fecund in the seaward plots.
4. The establishment of container-grown plants of four of the species was also compared at two sites at similar distances from the sea, but with sandy or shingle-dominated substrates, respectively. Again, greater growth on the coarser shingle substrate by three of the most characteristic shingle beach species reflected an apparent selective advantage. Thus, substrate physical composition was probably the primary determinant of differences in performance across the beach profile.
5. The use of container-grown plants to establish shingle vegetation resulted in low mortality, with rapid plant growth and establishment. Fertilizer and organic matter treatments were not generally cost-effective in establishing shingle beach vegetation from container-grown plants. The use of resources to recreate an appropriate substrate composition is of far greater importance.

Key-words: beach revegetation, fertilizer, organic matter, salinity, soil texture.

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Introduction

During the construction of Sizewell 'B' power station, we investigated methods for the restoration of the distinctive plant communities of the shingle beach and dunes that would be needed after the inevitable severe disturbance to about 1 km of coastline (Walmsley & Davy 1997a). Experiments to investigate the re-estab-

lishment of key species by direct sowing of seeds into the shingle beach substrate led to predictions of poor germination, poor establishment and high mortality for most species (Walmsley & Davy 1997b). Plants experienced high-temperature stress and desiccation in summer, and sea-water spray, burial and erosion in winter. Many environmental factors can prevent or delay seedling establishment in coastal localities (Maun 1994).

Beach species need to accumulate substantial

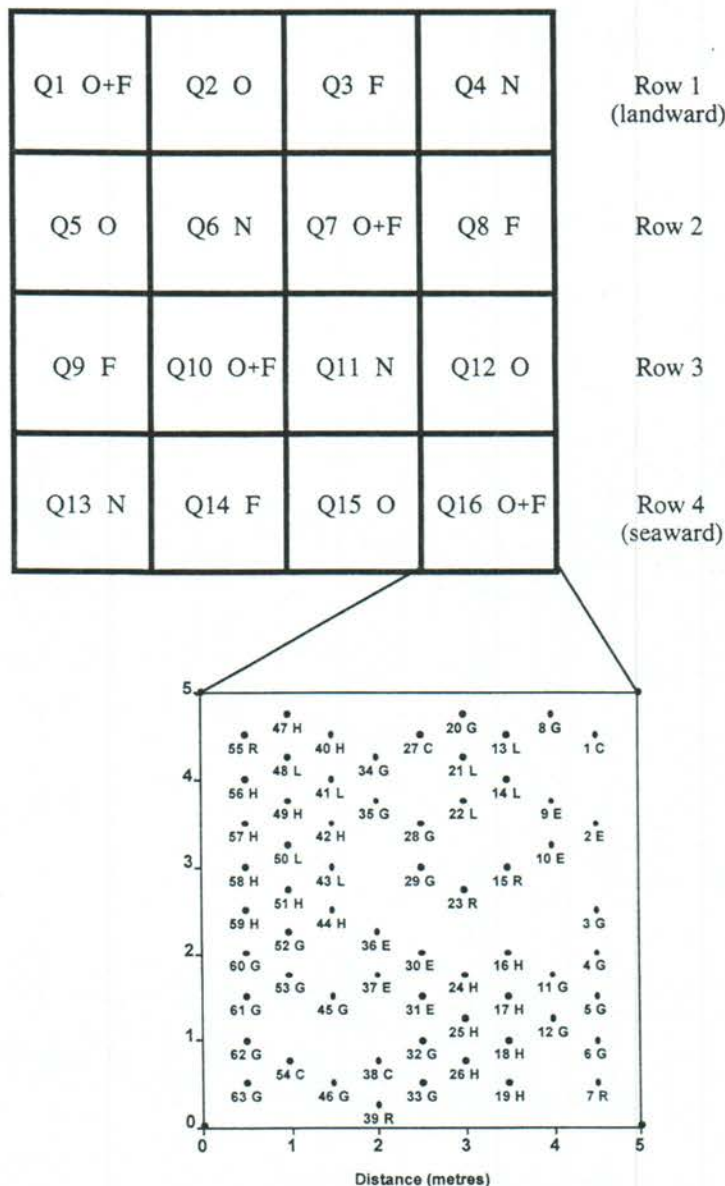


Fig. 1. Plan of the substrate amendment field experiment on the shingle beach at Sizewell, Suffolk: (a) the layout of quadrats, and (b) the layout of plants in each quadrat. Quadrats: Q1–Q4 (row 1), landward, sandy row; Q13–Q16 (row 4), seaward, predominantly shingle row. Planting treatment: N, untreated; F, fertilizer addition; O, organic matter addition; O + F, organic matter and fertilizer addition. The layout of plants is marked with the species and the sequence number of each plant. Species: C, *Crambe maritima*; E, *Eryngium maritimum*; G, *Glaucium flavum*; H, *Honckenya peploides*; L, *Lathyrus japonicus*; R, *Rumex crispus* ssp. *litoreus*.

All plants were watered on the 4 and 29 May 1990 as temperatures were high and precipitation was very low during May. The rainfall between May and August 1990 was 121 mm, 73% of the 5-year mean for 1989–93, but no further watering or maintenance was carried out.

Monitoring

The size of the plants was monitored by measuring leaf or stem lengths. Vegetative *G. flavum*, *E. maritimum*, *R. crispus* and *C. maritima* plants develop a basal leaf rosette and so the length of each individual leaf was measured. For *H. peploides* and *L. japonicus*,

the length of each shoot was measured from the tip of the uppermost leaf to the origin of the shoot at the base of the plant, or to the junction of the side shoot with the main axis. Mortality during the growing season was defined as the absence of any above-ground live leaves or shoots. *Crambe maritima*, *E. maritimum*, *L. japonicus* and *H. peploides* die back to ground level in autumn and, therefore, mortality could not be identified during winter. For reproductive plants, the maximum flowering stem height and the number of flowers and fruits were also recorded. All plants were measured shortly after planting in May, and also in late June and September 1990. In October 1990 the seed-pods of *G. flavum* and the inflorescences of *R.*

crispus were counted. Viability of the seed produced was assessed by germination tests (Walmsley & Davy 1997a). Severe burial and erosion as a result of storm tides in December 1990 prevented further monitoring of the amendment and location effects during 1991, although eventual plant re-emergence and growth after accretion and erosion were recorded and will be presented elsewhere.

Particle size analysis

Five soil-cores (100 mm diameter \times 130 mm) were taken from each of the four landward quadrats (Q1–Q4, see Fig. 1) and each of the four seaward quadrats (Q13–Q16, see Fig. 1) on 11 December 1990. The samples were air-dried in a laboratory and hand-sieved through 9.5-, 4- and 2-mm sieves. The < 2-mm separate was subsampled to obtain two 100–120 g sub-samples which were sieved through 1.0-, 0.5-, 0.25-, 0.125- and 0.063-mm sieves using an Endecotts mechanical shaker for 5 min. All separates were weighed to determine their relative proportions.

SUBSTRATE COMPOSITION FIELD EXPERIMENT

A field experiment to determine the effects of predominantly sandy or shingle substrates on the establishment of container-grown plants was planted between 21 and 23 April 1993. The experiment was laid out on two sites c. 70 m apart, both unvegetated and positioned a similar distance from the MHW. Both sites sloped seawards, ranging from 4.17–4.04 m above OD at the shingle site and 4.07–3.87 m above OD at the sand site. The mean site elevation was 4.11 ± 0.03 m above OD at the shingle site and 3.97 ± 0.06 m on the sand site. The only visible difference between the sites was the substrate; one site was almost entirely sand, while the other was mainly shingle with a small sand fraction, and hence they are referred to as the 'shingle' and 'sand' sites. Container-grown plants of *C. maritima*, *E. maritimum*, *G. flavum* and *R. crispus* were grown using the methods described previously and were 21 weeks old at planting. At both sites a 5 \times 5-m area was fenced and a 4 \times 4-m area within each was marked out into sixteen 1 \times 1-m subplots. Each subplot was planted with five plants of a single species in a quincunx pattern. Each species was planted in four of the 16 subplots at each site, such that each occurred once in every row and column of the 4 \times 4 matrix, giving a total of 20 plants of each species in each matrix. All plants were fertilized with a 3 g 'Agriform' container fertilizer tablet but there was no other maintenance. No watering was carried out: the rainfall between May and August 1993 was 177 mm, slightly greater than the 5-year mean for 1989–93. The size of the plants and their reproduction were monitored by measurement at monthly intervals between May and September 1993, using the methods described previously. Plants were harvested in Sep-

tember 1993, and partitioned into roots, rosette leaves, flowering stem and stem leaves, and seed pods. Material was dried at 70°C for 5 days before weighing. Sediment particle size was analysed for eight 1020-cm³ volume soil samples collected at each site at the time of planting.

Forty plants of each species were planted on a neighbouring area of shingle beach at the same time as the experiment. These plants were measured and harvested at various periods after planting, using the methods described above. Regressions of shoot biomass on total plant leaf length were produced. These provided an assessment of the validity of using leaf length measurements to determine changes in plant size in the experiments. They were also used to estimate shoot dry mass in the experiment without destructive harvesting.

STATISTICAL ANALYSIS

The significance of the row, column and treatment effects in the latin square design of the substrate amendment experiment was assessed separately for each species using ANOVA. For the substrate composition experiment the significance of the effects of substrate differences between the sites, and the effects of the plots within the shingle and sand sites was analysed; an analysis of covariance (ANCOVA) was carried out separately for each species, with the initial estimated shoot mass, derived from the regressions described below, used as a covariate to remove the effects of the plant size at the time of planting. Tukey's HSD multiple range test was used to compare means. Differences in mortality between treatments and rows were compared, assuming equal expected values, using χ^2 on a 1 \times 4 contingency table.

The best-fit regression between total plant leaf length and shoot biomass was achieved using a power function ($y = ax^b$) for all four species (Fig. 2); although the r^2 values were only slightly better than those for linear regression for *E. maritimum* and *R. crispus*. The non-linearity probably results from the development of a thickened basal stem with age in all of these rosette species. The estimated shoot mass corresponded well with the harvested shoot mass of *C. maritima*, but somewhat under-estimated the harvested shoot mass of the other species. The use of leaf length measurements to record plant size in both the experiments should provide a good indication of changes in shoot mass as high r^2 values indicate the close fit between total leaf length and shoot mass (Fig. 2).

Results

SUBSTRATE AMENDMENT FIELD EXPERIMENT

Substrate texture

The results of particle-size analyses of substrate samples from row 1 (Q1–4, Fig. 1) and row 4 (Q13–16) in

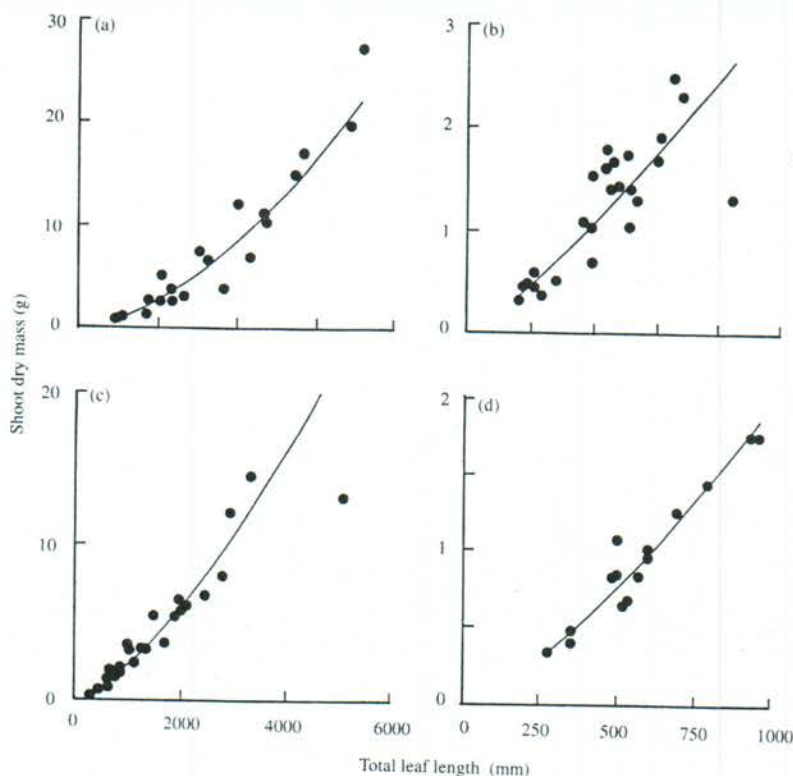


Fig. 2. Regression of shoot mass on total plant leaf length (of the form $y = ax^b$) for plants grown on the shingle beach at Sizewell, Suffolk, alongside the substrate composition experiment. The equations were used to estimate shoot mass non-destructively for this experiment (a) *Crambe maritima* (constants: $a = 1.365 \times 10^{-4}$, $b = 1.652$; $r^2 = 0.911$) (b) *Eryngium maritimum* ($a = 8.356 \times 10^{-4}$, $b = 1.197$; $r^2 = 0.805$) (c) *Glaucium flavum* ($a = 9.752 \times 10^{-5}$, $b = 1.450$; $r^2 = 0.918$) and (d) *Rumex crispus* ($a = 3.0 \times 10^{-4}$, $b = 1.293$; $r^2 = 0.852$).

the experiment are shown in Fig. 3. The substrate in the quadrats of rows 1–3 was a relatively homogenous sandy-shingle mixture, although at the seaward edge of the row 3 plots (Q9–12) the substrate was coarser and similar to that in the row 4 plots. There was also little obvious variation in substrate between quadrats in each row. However, there were very significant differences in the percentage by mass of particles 0.25–0.5 mm and > 9.5 mm diameter between the sandy row 1 and shingle-dominated row 4 plots (Fig. 3).

When the composition of the sand and silt fraction only was considered there was little difference in the particle-size composition between rows.

Plant survival

Survival during the first field-season was high; overall mortality was only 8%. *Crambe maritima*, *G. flavum*, *L. japonicus* and *R. crispus* showed very low mortality (Table 1). None of the species individually showed

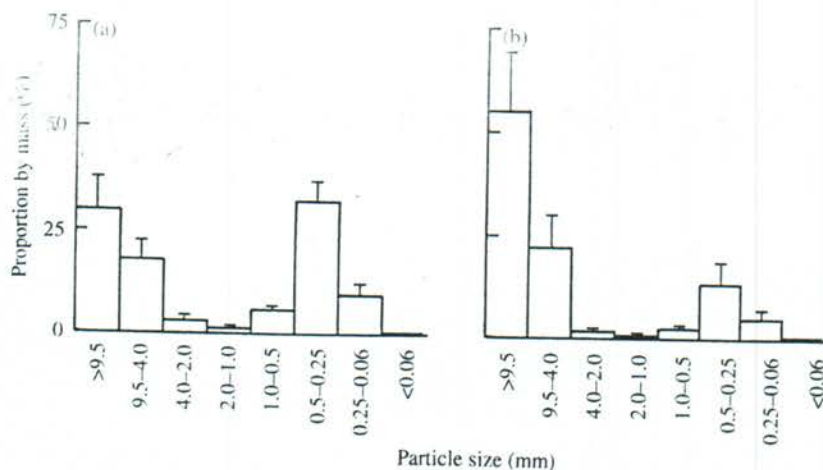


Fig. 3. Particle-size analyses of substrates from the substrate-amendment field experiment on the shingle beach at Sizewell, Suffolk: (a) the sandy, landward (row 1) plots; (b) shingle-dominated, seaward (row 4) plots. The mean percentage of the total sample by mass is shown for each particle-size class: error bars represent one SD.

Table 1. The effect of fertilizer and organic matter planting treatments and planting location on the mortality of container-grown transplants by the end of the first growing season (September 1990) at Sizewell, Suffolk. Number of deaths (percentage mortality in parentheses) are shown. The combined mortality for all species was compared between treatments and planting location using a χ^2 -test, as the numbers of deaths for individual species were too few for analysis

Species	Number of deaths in quadrats (% in parentheses)						Total		
	Untreated	Fertilizer	Organic matter	Organic matter and fertilizer	Row 1 Landward	Row 2		Row 3	Row 4 Seaward
<i>Crambe maritima</i>	1 (8)	0	1 (7)	1 (7)	0	1 (7)	0	2 (14)	3 (5)
<i>Eryngium maritimum</i>	1 (4)	2 (9)	5 (20)	5 (18)	1 (4)	3 (12)	3 (13)	6 (24)	13 (13)
<i>Glaucoium flavum</i>	6 (8)	1 (1)	0	1 (1)	0	2 (3)	3 (4)	3 (4)	8 (3)
<i>Honckenya peploides</i>	9 (19)	9 (17)	3 (6)	12 (21)	11 (18)	5 (10)	7 (14)	10 (20)	33 (16)
<i>Lathyrus japonicus</i>	4 (21)	0	0	1 (4)	1 (4)	0	1 (4)	3 (19)	5 (6)
<i>Rumex crispus</i>	1 (7)	0	0	1 (6)	0	1 (6)	0	1 (8)	2 (3)
Total	22 (11)	12 (6)	9 (4)	21 (9)	13 (6)	12 (6)	14 (7)	25 (12)	64 (8)

Treatment: $\chi^2 = 7.875$, d.f. 3, $P = 0.045$
Location: $\chi^2 = 6.875$, d.f. 3, $P = 0.08$

significant differences in mortality between planting treatments or planting location. However, all species showed higher mortality in the seaward, predominately coarse shingle plots (row 4) compared with the others. The organic matter substrate amendment significantly reduced total mortality (for all species) compared to untreated or fertilizer plus organic matter amendment (Table 1).

Plant growth

No significant differences had developed between plots by June and the results are not presented. The effects of the fertilizer and organic matter amendments on plant size after one season's growth in September 1990 are shown in Table 2 as mean total leaf or shoot length per plant. An ANOVA of plant size in September for each species revealed no significant differences as a result of planting treatment (Table 3). Although plants were grown in a mixed-species pattern, the spacing was such that interactions between them would have been very unlikely and, thus, the independence assumptions of ANOVA should not have been compromised. *G. flavum* plants were somewhat larger with all three amendments, *R. crispus* was substantially larger in organic matter treated plots and *L. japonicus* was substantially larger in untreated plots (Table 2). Overall, the fertilizer and organic matter amendments provided no significant benefit for plant growth.

The row effects in the latin square planting design showed that location on the beach was an important influence on plant growth (Tables 2 and 3). *G. flavum* and *R. crispus* grew significantly larger in the most seaward row of quadrats, and *C. maritima* plants were also largest in the seaward row. *Honckenya peploides* showed a progressive seaward increase in size.

Reproduction

Sixty *G. flavum* plants (19% of the population) produced reproductive shoots and subsequently seeds in the first field-growing season. The fertilizer treatment, either alone or in combination with organic matter, resulted in a greater percentage of reproductive *G. flavum* plants, but no treatment resulted in greater seed or seed pod production per plant relative to untreated plants (Table 4). The percentage of reproductive *G. flavum* plants was substantially greater in the seaward (row 4) plots. Moreover, the mean maximum flowering stem height, the mean number of seed-pods per plant, the mean number of seed-pods per quadrat and the mean estimated seed number per plant were all significantly greater in the seaward plots (Table 4).

Only 10 plants of *R. crispus* (17% of the population) became reproductive during the first field growing season. Hence, no statistically significant effects could be identified. However, like *G. flavum*, the percentage of reproductive plants was greater in the seaward plots

Table 2. The effect of fertilizer and organic matter planting treatments and planting location on the shingle beach on the size achieved by container-grown transplants by the end of the first growing season (September 1990) at Sizewell, Suffolk. Growth was recorded as total leaf or shoot length (mm). Significantly different mean values ($P < 0.05$), according to Tukey's multiple range test, are indicated by different letters in rows

Species	Mean total leaf or shoot length (mm) \pm SE							
	Untreated	Fertilizer	Organic matter	Organic matter and fertilizer	Row 1 Landward	Row 2	Row 3	Row 4 Seaward
<i>Crambe maritima</i>	677 \pm 101	574 \pm 76	612 \pm 74	706 \pm 87	614 \pm 54	499 \pm 25	666 \pm 119	791 \pm 25
<i>Eryngium maritimum</i>	397 \pm 73	419 \pm 31	337 \pm 116	383 \pm 100	314 \pm 97	531 \pm 58	314 \pm 71	377 \pm 50
<i>Glaucium flavum</i>	2091 \pm 486	2576 \pm 714	2600 \pm 341	2580 \pm 455	1981 \pm 254a	1570 \pm 172a	2641 \pm 240ab	3653 \pm 391b
<i>Honckenya peploides</i>	519 \pm 167	366 \pm 91	385 \pm 84	511 \pm 140	148 \pm 112a	471 \pm 65ab	568 \pm 138b	594 \pm 63b
<i>Lathyrus japonicus</i>	800 \pm 233	699 \pm 62	680 \pm 112	577 \pm 116	620 \pm 215	807 \pm 69	782 \pm 29	545 \pm 156
<i>Rumex crispus</i>	968 \pm 121	916 \pm 115	1382 \pm 438	1109 \pm 418	658 \pm 74a	828 \pm 36a	1026 \pm 165a	1863 \pm 344b

Table 3. Summary of the results of ANOVA of plant size achieved by container-grown transplants, recorded as total leaf or shoot length in September 1990, in the substrate amendment experiment on the shingle beach at Sizewell, Suffolk. Data shown are probabilities. A separate analysis was carried out for each species. The latin square design allows discrimination of treatment, row and column effects. Treatments: untreated, fertilizer, organic matter and organic matter plus fertilizer. Rows represent distance from the sea

Species	Column	Row	Treatment
<i>Crambe maritima</i>	0.504	0.317	0.124
<i>Eryngium maritimum</i>	0.908	0.954	0.937
<i>Glaucium flavum</i>	0.829	0.004	0.721
<i>Honckenya peploides</i>	0.283	0.004	0.495
<i>Lathyrus japonicus</i>	0.100	0.689	0.726
<i>Rumex crispus</i>	0.023	<0.001	0.242

and the fertilizer or fertilizer plus organic matter amended plots (Table 5). The total number of flowering stems and the number of fertile flowering stems was also greatest in the seaward plots. Six of the 15 flowering stems produced were abortive and produced no seeds. Petri-dish germination tests on seeds from the other nine inflorescences showed that only four inflorescences produced viable seed and only one produced a high percentage of viable seed. Most infertile seed contained no embryo.

Only one plant of *L. japonicus* flowered and produced 37 seeds in eight pods, and no *C. maritima*, *E. maritimum* and *H. peploides* plants became reproductive.

SUBSTRATE COMPOSITION FIELD EXPERIMENT

Substrate

The substrate of the shingle site contained very high percentages of 4.0–9.5-mm and > 9.5-mm diameter separates, while the sand site was predominantly composed of < 2-mm-diameter particles (Fig. 4). There were only small differences in the percentage composition of the separates within the < 2-mm fraction.

Plant survival

The total mortality rate during the first field growing season was low (7.5%). The survival of all 20 plants of *C. maritima* in the shingle plots was in contrast to the death of nine out of 20 plants in the sand plots. Almost all of this mortality occurred soon after planting during May. A total of three plants died among all the other three species at both shingle and sand sites.

Plant growth

The effect of the substrate on mean estimated shoot mass between April and September 1993 is shown in

Table 4. The effect of fertilizer and organic matter planting treatments and planting location on the shingle beach on reproduction of container-grown transplants of *Glaucomia fluitans* by the end of the first growing season (September 1990) at Sizewell, Suffolk. Different letters in a row indicate treatments or locations significantly different ($P < 0.05$) according to Tukey's multiple range test. The mean estimated seed number plant⁻¹ was calculated as: mean number of seed-pods per plant \times mean number of seeds per pod

	Untreated	Fertilizer	Organic matter	Organic matter and fertilizer	Row 1 Landward	Row 2	Row 3	Row 4 Seaward	Total
Number of reproductive plants (% in parentheses)	7 (9)	24 (32)	8 (10)	21 (26)	14 (19)	5 (7)	5 (11)	36 (44)	60 (19)
Mean max. flowering stem height (mm \pm SE)	430 \pm 10a	288 \pm 20b	191 \pm 35b	256 \pm 25b	187 \pm 18a	178 \pm 34a	254 \pm 45ab	335 \pm 17b	281 \pm 15
Mean number of seed-pods plant ⁻¹ (\pm SE)	20.7 \pm 5.7	17.5 \pm 2.6	5.6 \pm 1.7	17.5 \pm 3.7	6.5 \pm 1.1	7.2 \pm 2.0ab	16.2 \pm 3.8ab	21.4 \pm 2.7b	16.3 \pm 1.9
Mean number of seed-pods quadrat ⁻¹ (\pm SE)	36.3 \pm 36.3	105 \pm 76.6	11.25 \pm 7.0	92.25 \pm 62.3	23 \pm 13.3a	9.0 \pm 5.3a	20.25 \pm 14.6a	192.5 \pm 70.7b	61.2 \pm 51.2
Mean estimated seed number plant ⁻¹	5601	3906	1549	4816	1379	1527	3438	5791	4411

Table 5. The effect of fertilizer and organic matter planting treatments and planting location on the shingle beach on reproduction of container-grown transplants of *Rumex crispus* by the end of the first growing season (September 1990) at Sizewell, Suffolk. No values were significantly different ($P < 0.05$) according to Tukey's multiple range test

	Untreated	Fertilizer	Organic matter	Organic matter and fertilizer	Row 1 Landward	Row 2	Row 3	Row 4 Seaward	Total
Number of reproductive plants (% in parentheses)	1 (7)	3 (21)	2 (13)	4 (25)	1 (7)	3 (18)	1 (7)	5 (38)	10 (17)
Mean flowering stem height (mm \pm SE)	615	430.0 \pm 72	355.0 \pm 70	483.6 \pm 58	300	571 \pm 22	215	448 \pm 45	447 \pm 38
Mean inflorescence length (mm \pm SE)	440	216.7 \pm 58	223.7 \pm 50	304.3 \pm 59	100	370 \pm 47	90	281.5 \pm 40	274 \pm 35
Total no. of flowering stems (no. of fertile stems)	1 (1)	3 (0)	4 (3)	7 (5)	1 (0)	3 (2)	1 (0)	10 (7)	15 (9)
Mean seed number fertile flowering-stem ⁻¹ (\pm SE)	55	0	369 \pm 319	384 \pm 628	0	843.5 \pm 788	0	199 \pm 262	342 \pm 513

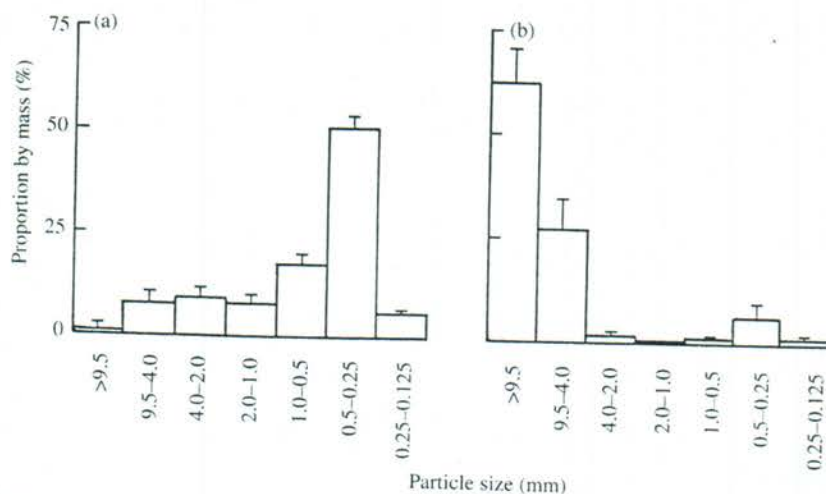


Fig. 4. Particle-size analyses of substrates from the substrate composition field experiment on the shingle beach at Sizewell, Suffolk: (a) sandy site; (b) shingle-dominated site. The mean percentage of the total sample by mass is shown for each particle-size class; error bars represent one SD.

Fig. 5. The increase in shoot biomass was greater in plants from the shingle site for all four species. *Crambe maritima*, *G. flavum* and *R. crispus* developed more leaves per plant at the shingle site (results not shown). *Eryngium maritimum* mean leaf number was almost identical in September 1993 at both sites.

The mean total plant mass harvested in September 1993 was substantially greater from the shingle site than from the sand site for *C. maritima*, *G. flavum* and

R. crispus, and similar at both sites for plants of *E. maritimum* (Fig. 6a). In those species that showed differential growth between sites both the roots and the shoots were significantly larger at the shingle site. The differences in allocation between roots and shoots varied little between sites, but greatly between species (Fig. 6b).

A summary of the results of the ANCOVA of harvested total plant mass is given in Table 6. Original

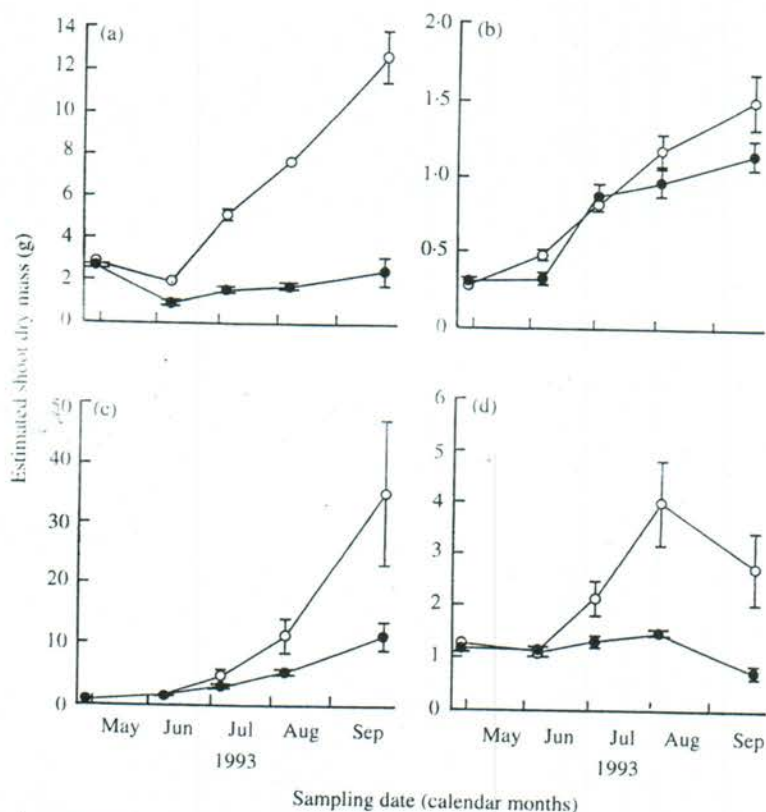


Fig. 5. The effect of substrate on mean estimated shoot dry mass of container-grown transplants during the first field growing season in the substrate composition field experiment at Sizewell, Suffolk: (a) *Crambe maritima*; (b) *Eryngium maritimum*; (c) *Glaucium flavum*; (d) *Rumex crispus*. Plantings on the shingle site (○) and on the sandy site (●). The experiment was planted on 21 and 22 April 1993. Error bars represent ± SE.

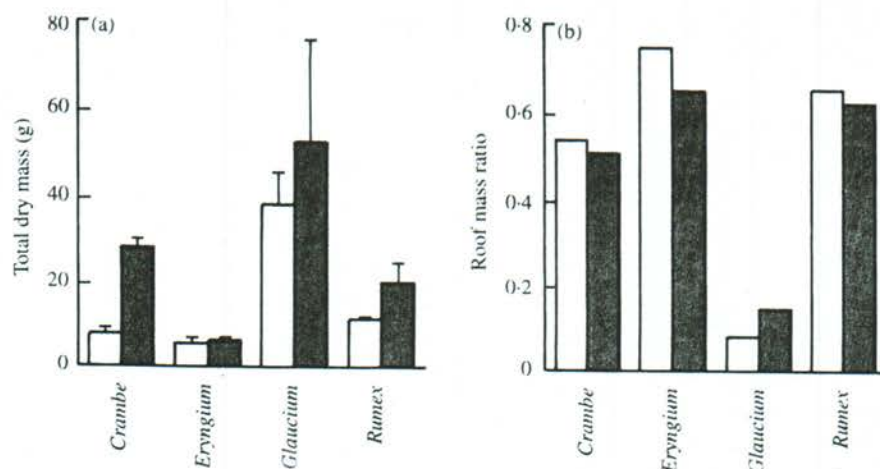


Fig. 6. The effect of substrate composition on the mean harvest dry mass of container-grown transplants at the end of the first field-growing season in the substrate composition field experiment at Sizewell, Suffolk: (a) total dry mass; (b) root mass ratio (root mass/total mass) of *Crambe maritima*, *Eryngium maritimum*, *Glaucium flavum* and *Rumex crispus* plants at the sandy site (unshaded) and shingle-dominated site (shaded bars). Plants were harvested on 23–26 September 1993. Error bars in (a) represent one SE.

shoot mass, the covariate in the ANCOVA, only had a significant effect on the harvested total plant mass of *R. crispus*. The substrate had a significant effect on the total plant mass of both *C. maritima* and *R. crispus*. There was significant variance in the harvested mass of *G. flavum* plants between plots at the shingle and sand sites (Table 6).

Reproduction

Forty-three per cent of the *G. flavum* plants in the experiment produced reproductive shoots during the first field season. There were similar numbers of reproductive *G. flavum* plants at both sites and they produced flowering stems of similar height (Table 7). Although the number of pods, mean reproductive shoot biomass and mean seed-pod mass per plant were all substantially greater for the shingle site, the variability within both sites was substantial. The reproductive shoot biomass comprised all of the har-

vested aerial stems arising from the rosette, including stem leaves and peduncles but excluding seed-pods. Only one *R. crispus* plant produced a reproductive shoot: this was in the shingle site, which produced significantly larger plants compared to the sand site. *Crambe maritima* and *E. maritimum* plants at both sites remained vegetative.

Discussion

None of the species demonstrated a significant growth response to fertilizer or organic matter additions in the substrate amendment experiment. The fertilizer tablets were slow-release and nitrogen-rich so that, in a potentially nitrogen-limited system (Salisbury 1922; Scott 1960), improved growth might have been anticipated. However, container-grown plants would have had substantial nutrient resources at the time of plant-

Table 6. Summary of the results of ANCOVA of plant dry mass achieved by container-grown transplants at harvest in September 1993, in the substrate composition experiment on the shingle beach at Sizewell, Suffolk. Data shown are probabilities. A separate analysis was carried out for each species. The initial estimated shoot dry mass was used as a covariate to remove variation due to plant size at the time of planting. It was derived using the best-fit regression (Fig. 2) between total plant leaf length and shoot biomass. The analysis allows discrimination of substrate (differences between the shingle and sand sites), plot (differences between plots within the sites) and covariate effects

Species	Covariate	Substrate	Plot
<i>Crambe maritima</i>	0.645	0.001	0.369
<i>Eryngium maritimum</i>	0.311	0.575	0.289
<i>Glaucium flavum</i>	0.831	0.243	0.038
<i>Rumex crispus</i>	0.044	0.022	0.229

Table 7. The effect of substrate on reproduction of *G. flavum* in the shingle-dominated and sandy sites at the end of the first field-growing season in September 1993 in the substrate composition field experiment on the shingle beach at Sizewell, Suffolk. The reproductive shoot biomass comprised all of the harvested aerial stems arising from the rosette, including all stem leaves and peduncles, but excluding seed-pods

	Shingle site	Sand site
Number of reproductive plants (% in parentheses)	8 (40)	9 (45)
Mean flowering stem height plant ⁻¹ (mm ± SE)	433 ± 19.4	406 ± 29.7
Number of seed-pods plant ⁻¹ (pods ± SE)	27.7 ± 12.2	20.8 ± 4.5
Mean reproductive shoot biomass plant ⁻¹ (g ± SE)	18.6 ± 10.7	9.8 ± 2.6
Mean seed-pod biomass plant ⁻¹ (g ± SE)	21.9 ± 13.2	10.0 ± 2.5

ing, and so would have taken some time to become nutrient-limited in the field, by which time the fertilizer may have been leached. Nutrient additions would be leached rapidly from the very porous shingle substrate and would inevitably have only a short-term impact. Therefore, the flux of nutrients through the substrate would probably be of relatively greater importance than in most soils. Scott (1960) considered percolating rainfall an important source of plant nutrition on shingle beaches; with the current high rates of NO_3 deposition in SE England due to acid rain (Bell 1993), this would now be of even greater importance. Another potential source of nitrogen was nitrogen-fixing nodules that were observed on the roots of *L. japonicus* plants in the field experiment. N_2 -fixation may increase the nitrogen status of the beach, but probably not within the time-scale of the experiment. However, measurements on dunes in North America showed that N_2 -fixation in *L. japonicus* contributes only $6 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (Bublitz 1982) and the nodules are never numerous in Britain according to Brightmore & White (1963). Mortality was low in all treatments, but was lowest in the organic matter treatment, except for *E. maritimum*. The organic matter presumably improved moisture retention and reduced plant water stress, aiding survival, although not increasing growth.

The greater growth of four of the six species in the seaward-most plots of the amendment experiment could in principle have been the result of the differences in substrate composition or nearness to the sea. Growth of *H. peploides* increased progressively seawards, suggesting an effect of the sea, whereas *G. flavum* and *R. crispus* grew larger solely in the coarse substrate of the seaward row of quadrats. Marine influences such as substrate erosion or accretion and sea-water inundation were not relevant from the time of planting until the end of the growing season. No significant amounts of drift material, which could improve growth, were observed in the seaward plots at the time of planting. Salt-spray intensity is an important factor controlling the distribution of plants on beaches, although deposition of salt-spray declines rapidly with distance from the sea (Oosting & Billings 1942; Oosting 1945; Boyce 1954; van der Valk 1974; Barbour 1978). Salt-spray can also provide an important nutrient input, particularly of NO_3^- , which may invoke positive growth responses to salt-spray (Rozema *et al.* 1982; Lee & Ignaciuk 1985). Given the low nutrient status of the shingle, the growth response shown by *H. peploides* might have been a result of improved long-term nutrient flux. The *R. crispus* plants at the seaward edge of the substrate amendment experiment had the greatest mean plant size and showed almost no leaf damage. Yet the substrate composition experiment showed *R. crispus* to be a sensitive indicator of salt-spray; onshore gales in the spring of 1993 caused significant leaf burn and reduced mean leaf number per plant. This suggests that salt-spray was not important during the growing season of 1990

and, therefore, the effects of substrate composition may be more important.

The experiment on shingle and sand sites clearly showed the importance of an appropriate beach substrate for plant growth and survival. Growth responses indicate that the characteristic dune species, *E. maritimum*, was indifferent to the texture of the substrate, but the typical shingle beach species, *R. crispus*, *C. maritima* and *G. flavum*, performed much better on a predominantly shingle substrate. The mechanism of this response is unknown, but both *C. maritima* (Scott & Randall 1976) and *G. flavum* (Scott 1963b) are associated with well drained substrates. The major differences in growth related to planting location in the amendment experiment were probably also primarily the result of such substrate effects. The slightly greater mortality in the seaward quadrats was almost certainly the result of the coarse shingle substrate, which had a low moisture retention capacity and so allowed water stress. Wilting was observed during May and June 1990, especially on the coarse substrates. It is likely that organic matter reduced water-stress and so ameliorated mortality, particularly in coarse shingle, but there was insufficient mortality to determine statistically whether this was the case. The death of *C. maritima* plants specifically at the sandy site was clearly the result of sand-blasting during strong winds that caused fatal leaf and shoot damage. *G. flavum* and *R. crispus* also suffered some leaf damage as a result of sand-blasting, but *C. maritima* appeared to be particularly sensitive to abrasion. Much less sand-blasting occurred in areas with a predominantly coarse shingle surface, presumably because sand particles landing on coarse shingle are lost in voids and removed from the aeolian transportation process.

The greater reproductive capacity and percentage of reproductive *G. flavum* plants in the seaward quadrats may have been a result of both location and substrate effects, as the percentage of reproductive plants on both substrates was similar, but the shingle site plants produced a greater reproductive shoot biomass and more seed-pods. The greater percentage of reproductive plants in fertilized plots suggests that nutritional differences as a result of proximity to the sea may also have contributed to the greater percentage of reproductive plants in the seaward quadrats.

The re-establishment of shingle beach species using container-grown plants was extremely successful. Mortality was low and growth good, particularly on the more appropriate substrates. There is evidence that the short-lived *G. flavum* established potentially self-sustaining populations and no obvious reason why the perennials should not do so in the longer term. It appears that there is little justification for applying fertilizer or incorporating organic matter into the substrate when using container-grown plants, especially in view of the cost and effort involved. The

use of resources to create an appropriate substrate composition and beach profile is more important. Substrate texture is critical for the establishment and success of most of these species. Clearly, beach sand, rather than imported organic matter, is more cost-effective and closer to natural conditions for improving water retention, where necessary. There are advantages in a mosaic of textures: coarse-textured shingle is generally appropriate for the established plants and helps to maintain the characteristically sparse nature of the vegetation; patches with up to about 20% sand content would be helpful for regeneration from seed (Walmsley & Davy 1997b) and for maintaining the diversity of arenicolous or dune species commonly associated with shingle beaches. The creation of a matrix of areas with varying soil texture has also been advocated to aid the restoration of the characteristic mosaic of species in otherwise very different woodland systems (Packham *et al.* 1995).

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References

- Barbour, M.G. (1978) Salt spray as a microenvironmental factor in the distribution of beach plants at Point Reyes, California. *Oecologia*, **32**, 213–224.
- Beach Protection Authority, Queensland (1980–1990) *Dune stabilization and management research program*. Reports 1–4. Government Printer, Queensland.
- Bell, N. (1993) *The Ecological Effects of Increased Aerial Deposition of Nitrogen*. British Ecological Society Ecological Issues No.5. Field Studies Council, Shrewsbury.
- Boyce, S.G. (1954) The salt spray community. *Ecological Monographs*, **24**, 29–67.
- Brightmore, D. & White, P.H.F. (1963) Biological flora of the British Isles. *Lathyrus japonicus* Willd. *Journal of Ecology*, **51**, 795–801.
- Bublitz, A.E. (1982) *Ecological physiology of Lathyrus japonicus: nitrogen fixation, growth and water relations*. PhD thesis, Harvard University.
- Buckley, G.P. (1989) *Biological Habitat Reconstruction*. Belhaven Press, London.
- Ferry, B.W., Barlow, S.L. & Waters, S.J.P. (1989) The shingle ridge succession at Dungeness. *Botanical Journal of the Linnean Society*, **101**, 19–30.
- Fuller, R.M. (1975) The Culbin shingle bar and its vegetation. *Transactions of the Botanical Society of Edinburgh*, **42**, 293–305.
- Fuller, R.M. (1987) Vegetation establishment on shingle beaches. *Journal of Ecology*, **75**, 1077–1089.
- Heath, S.E. (1981) A brief survey of the botany at Shingle Street, Suffolk. *Transactions of the Suffolk Naturalists' Society*, **18**, 249–253.
- Keddy, P.A. & Constabel, P. (1986) Germination of ten shoreline plants in relation to seed size, soil particle size and water level: an experimental study. *Journal of Ecology*, **74**, 133–141.
- Lee, J.A., Harmer, R. & Ignaciuk, R. (1983) Nitrogen as a limiting factor in plant communities. *Nitrogen as an Ecological Factor* (eds J.A. Lee, S. McNeil & I.H. Rorison), pp. 95–112. Blackwell Scientific Publications, Oxford.
- Lee, J.A. & Ignaciuk, R. (1985) The physiological ecology of strandline plants. *Vegetatio*, **62**, 319–326.
- Maun, M.A. (1994) Adaptations enhancing survival and establishment of seedlings on coastal dune systems. *Vegetatio*, **111**, 59–70.
- Oliver, F.W. (1912) The shingle beach as a plant habitat. *New Phytologist*, **11**, 75–99.
- Oosting, H.J. (1945) Tolerance to salt spray of plants of coastal dunes. *Ecology*, **26**, 85–89.
- Oosting, H.J. & Billings, W.D. (1942) Factors affecting vegetational zonation on coastal dunes. *Ecology*, **23**, 131–142.
- Packham, J.R., Cohn, E.V.J., Millett, P. & Trueman, I.C. (1995) Introduction of plants and manipulation of field layer vegetation. *The Ecology of Woodland Creation* (ed. R. Ferris-Kaan), pp. 129–148. John Wiley & Sons, London.
- Randall, R.E. (1977) Shingle formations. *The Coastline* (ed. R.S.K. Barnes), pp. 199–213. John Wiley & Sons, London.
- Rozema, J., Bijl, F., Dueck, T. & Wesselman, H. (1982) Salt-spray stimulated growth in strand-line species. *Physiologia Plantarum*, **56**, 204–210.
- Salisbury, E.J. (1922) The soils of Blakeney Point: a study of soil reaction and succession in relation to the plant covering. *Annals of Botany* (old series), **36**, 391–431.
- Scott, G.A.M. (1960) *The biology of shingle beach plants with special reference to the ecology of selected species*. PhD thesis, University of Wales.
- Scott, G.A.M. (1963a) The ecology of shingle beach plants. *Journal of Ecology*, **51**, 517–527.
- Scott, G.A.M. (1963b) Biological flora of the British Isles. *Glaucium flavum* Crantz. *Journal of Ecology*, **51**, 743–753.
- Scott, G.A.M. & Randall, R.E. (1976) Biological flora of the British Isles. *Crambe maritima* L. *Journal of Ecology*, **64**, 1077–1091.
- Stace, C.A. (1991) *New Flora of the British Isles*. Cambridge University Press, Cambridge.
- Valk, A.G., van der (1974) Environmental factors controlling the distribution of forbs on coastal foredunes in Cape Hatteras National Seashore. *Canadian Journal of Botany*, **52**, 1057–1073.
- Walmsley, C.A. & Davy, A.J. (1997a) Germination characteristics of shingle-beach species, effects of seed ageing and their implications for vegetation restoration. *Journal of Applied Ecology*, **34**, 131–142.
- Walmsley, C.A. & Davy, A.J. (1997b) The restoration of coastal shingle vegetation: effects of substrate composition on the establishment of seedlings. *Journal of Applied Ecology*, **34**, 143–153.
- Wells, T.C.E., Cox, R. & Frost, A. (1989) *The Establishment and Management of Wildflower Meadows*. Focus on Nature Conservation, no. 21. Nature Conservancy Council, Peterborough.

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Contents

Essay Review

- 1 A. D. FOX & J. MADSEN. Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design
- 14 L. J. SANGER, P. COX, P. SPLATT, M. J. WHELAN & J. M. ANDERSON. The characterization of a lignin-derived organic matter fraction in soils developed under different vegetation types
- 21 S. JOHNSEN, A. P. GUTIERREZ & J. JØRGENSEN. Overwintering in the cabbage root fly *Delia radicum*: a dynamic model of temperature-dependent dormancy and post-dormancy development
- 29 M. A. PAGNOTTA, R. W. SNAYDON & P. S. COCKS. The effects of environmental factors on components and attributes of a Mediterranean grassland
- 43 P. M. THOMPSON, D. J. TOLLIT, D. WOOD, H. M. CORPE, P. S. HAMMOND & A. MACKAY. Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland
- 53 H. SMITH, K. MCCALLUM & D. W. MACDONALD. Experimental comparison of the nature conservation value, productivity and ease of management of a conventional and a more species-rich grass ley
- 65 D. ARSENAULT, N. VILLENEUVE, C. BOISMENU, Y. LEBLANC & J. DESHAYE. Estimating lichen biomass and caribou grazing on the wintering grounds of Northern Québec: an application of fire history and Landsat data
- 79 R. T. COOK, S. E. R. BAILEY & C. R. MCCROHAN. The potential for common weeds to reduce slug damage to winter wheat: laboratory and field studies
- 88 P. E. HATCHER, N. D. PAUL, P. G. AYRES & J. B. WHITTAKER. Added soil nitrogen does not allow *Rumex obtusifolius* to escape the effects of insect-fungus interactions
- 101 J. SALMINEN & J. HAIMI. Effects of pentachlorophenol on soil organisms and decomposition in forest soil
- 111 A. M. O'CONNELL. Decomposition of slash residues in thinned regrowth eucalypt forest in Western Australia
- 123 F. DESSAINT, R. CHADOUEF & G. BARRALIS. Nine years' soil seed bank and weed vegetation relationships in an arable field without weed control
- 131 C. A. WALMSLEY & A. J. DAVY. Germination characteristics of shingle beach species, effects of seed ageing and their implications for vegetation restoration
- 143 C. A. WALMSLEY & A. J. DAVY. The restoration of coastal shingle vegetation: effects of substrate composition on the establishment of seedlings
- 154 C. A. WALMSLEY & A. J. DAVY. The restoration of coastal shingle vegetation: effects of substrate composition on the establishment of container-grown plants
- 166 H. M. ARMSTRONG, I. J. GORDON, N. J. HUTCHINGS, A. W. ILLIUS, J. A. MILNE & A. R. SIBBALD. A model of the grazing of hill vegetation by sheep in the UK. I. The prediction of vegetation biomass
- 186 H. M. ARMSTRONG, I. J. GORDON, N. J. HUTCHINGS, A. W. ILLIUS, J. A. MILNE & A. R. SIBBALD. A model of the grazing of hill vegetation by sheep in the UK. II. The prediction of offtake by sheep
- 207 S. C. UREN, N. AINSWORTH, S. A. POWER, D. A. COUSINS, L. M. HUXEDURP & M. R. ASHMORE. Long-term effects of ammonium sulphate on *Calluna vulgaris*
- 217 N. M. VAN STRAALLEN & H. A. VERHOEF. The development of a bioindicator system for soil acidity based on arthropod pH preferences
- 233 H. JACHMANN & M. BILLIOUW. Elephant poaching and law enforcement in the central Luangwa Valley, Zambia
- 245 R. F. W. BARNES & S. A. LAHM. An ecological perspective in human densities in the central African forests
- 261 Book Reviews
- 270 Erratum
- 271 Instructions for Contributors

Certain papers in this issue were edited by former editors Nigel Webb or H. A. P. Ingram

b

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