

A comparison of regeneration dynamics following gap creation at two geographically contrasting heathland sites

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Summary

1. Lowland *Calluna*-dominated heathlands are a high priority for conservation in Europe. As an anthropogenic subclimax community they require regular management intervention to maintain their conservation interest.

2. Increasingly, *Calluna* is disappearing from lowland heathlands and being replaced by grasses, especially in the Netherlands and more recently in south-east England. While *Calluna* is highly competitive over much of its life cycle, its competitive ability is reduced during the regeneration phase that follows the death of stands or results from management activity.

3. We examined the influence of five factors on regeneration of vegetation in gaps in two broadly similar lowland dry heaths over a 3-year period. These were: geographical location (combining a variety of environmental contrasts); dominant species (*Calluna* or grasses); management techniques; gap size; and seed source availability.

4. Site location had the greatest effect on patterns of regeneration. Regeneration on the Wirral (north-west England) was faster and more dominated by *Calluna* than regeneration in Breckland (south-east England), which was dominated by other species including grasses and annual plants. Addition of *Calluna* seed at the Breckland site failed to increase *Calluna* cover. It was concluded that climatic or other environmental factors were the most probable cause of poor regeneration.

5. Cover of grasses in regenerating areas was greatest in Breckland, where *Deschampsia* was able to establish in all gaps where there was a seed source (either in the surrounding vegetation or applied as a treatment). On the Wirral, *Deschampsia* establishment was limited, even in gaps where a seed source was applied.

6. This work has implications for the conservation management of heathlands, which currently follows a standard prescription throughout the UK. It is suggested that management regimes should be tailored to suit the conditions prevailing at individual sites as regeneration dynamics may be extremely variable.

Key-words: *Calluna vulgaris*, conservation management, *Deschampsia flexuosa*, establishment, vegetation dynamics.

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Introduction

Dwarf shrub-dominated lowland heathlands are a subclimax community found throughout Britain and

coastal parts of Europe. They are especially well represented in Britain, which holds approximately 20% of the European total (Farrell 1989). Within the British Isles a range of dwarf shrub heathland types can be found, from wet heath dominated by *Erica tetralix* through the intermediate humid heaths to drier *Calluna vulgaris*-dominated communities. (For clarity *Calluna vulgaris* is referred to as

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Calluna throughout this paper. Nomenclature for plants follows Stace 1991.) In addition, the associated heathland flora shows wide variation both between heathland types and from one geographical region to another (Rodwell 1991). Due to the damp, mild subAtlantic climate in Britain, wet and humid heaths are particularly common, although dry heath occurs in areas with a suitable substrate and climate. The Breckland of East Anglia is the driest and most continental (in terms of both climate and vegetation) heathland area in Britain (Webb 1986; Farrell 1989; Rodwell 1991).

Since the 1700s, there has been a dramatic decline in heathland area throughout Europe (Farrell 1989). Heathlands were once widespread on sandy soils too poor to cultivate, which provided areas for grazing and the gathering of wood or turf for fuel. From the late 1700s onwards, expansion of agriculture resulted in many heaths being converted to arable or grassland. There were also losses as a result of the encroachment of forestry and the expansion of urban areas (Gimingham 1992). Traditional heathland management has ceased in many areas and surviving heaths have suffered invasion by late successional species such as bracken and trees (Marrs, Hicks & Fuller 1986; Marrs 1993). Most of the remaining lowland heathland is found within areas designated for nature conservation.

Since the early 1980s, there has been concern over the large amount of *Calluna* heath that has become dominated by grasses, often just a single species and typically *Deschampsia flexuosa* (hereafter referred to as *Deschampsia*) or *Molinia caerulea*. Increased grass dominance is known to occur as a result of overgrazing (Miles 1988) but, in these cases, has occurred on heaths with little or no grazing pressure. This phenomenon was first reported in the Netherlands, where heathland to grassland transitions occurred rapidly, often within 2–3 years (Heil & Diemont 1983). It is estimated that over 30% of Dutch heathlands are now dominated by grassland (Heil & Aerts 1993). During the 1990s, there have been reports from British heathland managers of similar changes on heaths in the south-east of England (Pitcairn, Fowler & Grace 1991; Dolman & Sutherland 1992; Marrs 1993).

The cause of the perceived increase of grasses on heathlands in south-eastern Britain is as yet unclear and there are a number of possible factors that may be involved. The growth cycle of *Calluna* on dry heaths, as described by Gimingham (1972), has important effects on the establishment and growth of associated species. During the building and mature phases, *Calluna* forms a closed canopy and is able to suppress its competitors almost entirely. Experimental work has shown that during this phase grasses are unable to replace *Calluna* directly unless the *Calluna* is damaged or defoliated in some way (Aerts *et al.* 1990; Van der Eerden *et al.* 1991).

However, during the late mature phase, the canopy becomes increasingly open, allowing more light to reach the ground and other species to invade. It is during the late building and early mature stage that management is usually timed to intervene, generally resulting in the creation of bare ground by cutting, burning or turf stripping. Where adult plants are killed or removed, *Calluna* seedlings can be slow to establish and may take up to 10 years to reach the fast-growing competitive building phase (Marrs 1986). Vegetative regrowth may also take several years to refill gaps in the canopy. During this period, where *Calluna* canopy cover is absent or much reduced, there is a window of opportunity for other species such as grasses to establish and become dominant. Grasses such as *Deschampsia* gain dominance rapidly and, once established, may shade out the young shade-intolerant *Calluna* plants. Thus it seems likely that the regeneration phase, following management activity or the death of plants, is the most likely point in the *Calluna* cycle for changes in species composition to occur. This fact presents a quandary for heathland managers because management is essential to maintain the heath but may also allow undesirable species composition changes to occur.

A number of factors are likely to affect regeneration dynamics and species composition following regeneration, particularly climate, management practices, soil properties, nutrient availability and seed inputs. Reports of grass invasion on lowland heathlands have so far been limited to the south-east of England and especially the Breckland region of East Anglia. The climate in this area is the most continental climate of any part of the UK, and in places is similar to the climate found in the Netherlands where grass invasions have occurred. However, mean annual rainfall is generally lower in the Brecklands (550 mm in Breckland compared with around 700 mm in the Netherlands; Wallén 1970). The continental climate includes hot dry summers, cold winters and a high chance of frost throughout the year, all three factors that are known to cause catastrophic death of *Calluna* (Marrs 1986). In addition, the Breckland experiences high levels of nitrogen deposition, especially as dry deposition (Pitcairn, Fowler & Grace 1991). Total values for nitrogen deposition may exceed 35–80 kg N ha⁻¹ year⁻¹, approaching the values recorded in continental Europe.

The main limiting factor for occupation of canopy gaps by grasses such as *Deschampsia* is the ability of the plants to colonize and establish in the gaps before *Calluna* becomes dominant once more. It might be expected that large gaps with a low edge : area ratio would persist for longer than small gaps (Denslow 1985), especially where plants within the gap have been killed or removed, and hence have a higher probability of species establishing from seed.

Proximity of gaps to existing *Deschampsia* patches (as a source of propagules) could also be important (MacArthur & Wilson 1967). The management method responsible for creating the gap may have some effect on regeneration; within the heathland system grasses are often associated with areas of slightly more fertile soil or where nutrient enrichment has occurred. Some management practices where the soil is disturbed may result in a pulse of nutrients. It might be expected, therefore, that management that creates a very nutrient-poor substrate would result in more favourable conditions for continued *Calluna* cover.

We examined the influence of geographical location (combining climatic, soil and nitrogen deposition differences), vegetation type, management methods, gap size and seed availability on the regeneration of heathland vegetation.

Materials and methods

STUDY AREAS

This experiment was replicated at two geographically separated sites in the UK, in order to achieve a contrast of environmental factors, including climate. Experimental sites were chosen to keep differences in vegetation and soils to a minimum. A comparison of soil properties at the two sites is given in Table 1. Both sites had a *Calluna*-dominated dry heath vegetation growing on free-draining, acid, sandy soils. They were Cavenham Heath National Nature Reserve (NNR) in Suffolk (0°34'E, 52°19'N, Ordnance Survey grid reference TL 7572) and Thurstaston Common Site of Special Scientific Interest (SSSI) in Merseyside (3°8'W, 53°21'N, Ordnance Survey grid reference SJ 2485).

Cavenham Heath is typical of many Breckland heaths. It is fairly flat with sandy soils formed from glacial sands and gravels that overlie a chalk bedrock. The heath is 230 ha in total, comprising areas of birch *Betula* sp. woodland, bracken *Pteridium aquilinum*, *Calluna* heath and acid grassland communities. Cavenham has a subcontinental climate with

low rainfall (mean 548 mm per annum), hot summers (mean maximum air temperature in July 21.7 °C) and cold dry winters (mean maximum air temperature in January 5.8 °C). Ground or air frost may occur on almost any day of the year (Trist 1979; climate data for Mildenhall 1916–50, grid reference TL 7175, 6 km north-west of Cavenham Heath). The area experiences a high nitrogen input (35–80 kg N ha⁻¹ year⁻¹), mainly in the form of dry deposition (Pitcairn, Fowler & Grace 1991).

Thurstaston Common is located on the western side of the Wirral and consists of 75 ha of birch woodland and *Calluna*-dominated heath. The soils of this area are sandy and free-draining, derived from the underlying Triassic sandstone. Thurstaston has the typical Atlantic climate of a site close to the sea on the western coast of Britain. It experiences moderate rainfall throughout the year (mean annual rainfall 720 mm) with warm summers (mean maximum air temperature in July 20.3 °C) and mild winters (mean maximum air temperature in January 7.1 °C) (climate data from Ness Botanic Gardens weather station 1966–98, Ordnance Survey grid reference SJ 3075, 9 km to the south of Thurstaston). Nitrogen deposition levels are relatively low, in the region of 10–15 kg N ha⁻¹ year⁻¹ (Bell 1994), and occur primarily as wet deposition.

EXPERIMENTAL DESIGN

The influence of five variables on vegetation development following gap creation was investigated in this field experiment. These were: geographical location, vegetation type, gap size, management type and addition of seed.

At both the Cavenham and Thurstaston sites, gaps were created in the existing vegetation and subsequent regeneration was recorded. At Cavenham, the experiment was established on two vegetation types, *Calluna*-dominated heath and *Deschampsia*-dominated grassland; at Thurstaston only the *Calluna*-dominated heath was present and a single set of experimental plots was set up. Similar mature *Calluna* stands were selected at the two sites. The

Table 1. Comparison of soil properties at Cavenham Heath and Thurstaston Common. Data for Cavenham Heath are from Marrs *et al.* (1992) and data for Thurstaston Common are from Goddard (1999)

Property	Thurstaston Common	Cavenham Heath
Depth of soil used (cm)	0–21	0–15
pH	3.8–4.0	3.6 ± 0.05
% loss of weight on ignition	7–15	7.2 ± 0.8
Extractable P (µg g ⁻¹ soil)	5–35	8.1 ± 0.8
Exchangeable elements (µg g ⁻¹ soil)		
K	75–105	24.8 ± 9.4
Ca	120–170	47.7 ± 9.5
Mg	45–55	5.9 ± 2.0

experiment was viewed as three 'blocks': Cavenham-*Calluna*, Cavenham-*Deschampsia* and Thurstaston-*Calluna*. The remaining factors: management, gap size and seeding were nested within these three blocks.

Within blocks, the experiment used a fully factorial design with three management types used to create gaps (cut, turf-stripped and rotavated), three gap sizes (1 m², 0.25 m² and 0.0625 m² square plots) and seeded and unseeded plots. In the cutting treatment the sward was clipped down to soil level and the plant material removed. In rotavated plots the sward was clipped to ground level and roughly chopped. The top 15 cm of the soil was then inverted and broken up with a spade, and the chopped plant material was mixed into the soil. For the turf-stripping treatment, the sward and underlying organic matter (including the L, F and H horizons) were removed to a depth of about 10 cm, exposing the sandy subsoil beneath. Cut turves were removed from the site. The seeding treatment was reciprocal, *Calluna* seed was only added to gaps in *Deschampsia* vegetation and *Deschampsia* seed added to gaps in *Calluna*. Native English seed of both species was obtained from a commercial supplier (John Chambers Wildflower Seeds, Barton Seagrave, UK). Rates of 35 000 seeds m⁻² for *Calluna* and 20 000 seeds m⁻² for *Deschampsia* were used, which had been calculated to be approximately equivalent to 1 year of seed rain at these sites, based on the observed density of flowering plants and the number of flowers per plant. Plots were spread randomly across the site within the designated vegetation types. There were three replicates of each treatment combination within each block.

The experiment was set up during March 1996 and subsequent recording of the vegetation regeneration was undertaken twice yearly at the beginning and end of the growing season (approximately April and October). A grid of 5 × 5-cm cells was placed over each gap and the species present in each square noted in four categories: *Calluna*, *Deschampsia*, other species and bare ground. The 'other species' category typically included *Betula* sp., *Carex arenaria*, *Festuca rubra*, *Galium* sp. and *Rumex acetosella* at Cavenham Heath, and *Betula* sp., *Hieracium* sp., *Pinus sylvestris*, *Pteridium aquilinum* and *Ulex* sp. at Thurstaston Common. Results were expressed as the percentage of the total cell number occupied by each species group. Analysis was conducted on arcsin square root-transformed data using repeated-measures ANOVA (Proc ANOVA; SAS Institute Inc. 1988). The effects of location were tested using treatment means from *Calluna* blocks at Cavenham and Thurstaston. Effects of vegetation type were tested using means from *Calluna* and *Deschampsia* blocks at Cavenham. All other treatments (gap size, management, seeding) were tested independently for each block using raw data. Bonferroni least signifi-

cant differences (SAS Institute Inc. 1988) were used to compare treatment means.

Results

GEOGRAPHIC LOCATION

The results of the between-sites analysis of vegetation development in *Calluna* stands at Thurstaston and Cavenham are shown in Fig. 1. All species groups showed significant differences between sites. The biggest difference was seen for *Calluna* ($F_{1,17} = 107.86$, $P = 0.0001$), which had an approximately fourfold greater frequency at Thurstaston than Cavenham after 3 years. The frequency of bare ground was reduced faster at Thurstaston and by the end of the third year was significantly less ($F_{1,17} = 13.37$, $P = 0.002$) than on the Cavenham plots. Thurstaston also had a significantly lower frequency of *Deschampsia* ($F_{1,17} = 16.29$, $P = 0.0009$) and other species ($F_{1,17} = 9.54$, $P = 0.0067$) over the 3-year period taken as a whole.

VEGETATION TYPE

An analysis between *Calluna* and *Deschampsia* vegetation types at Cavenham (Fig. 2) showed that all of the species groups had significant differences between the two vegetation types. The biggest difference between the vegetation developing in gaps in the two blocks was the higher frequency of *Calluna* in gaps in the *Calluna* vegetation type ($F_{1,17} = 55.17$, $P = 0.0001$ for a difference over 3 years). *Deschampsia* gaps had almost no *Calluna* at the end of 3 years. *Deschampsia* frequency was significantly greater ($F_{1,17} = 8.07$, $P = 0.0113$) over the whole 3-year period in gaps in the *Deschampsia* vegetation type, and the frequency of 'other' species was also significantly greater ($F_{1,17} = 10.40$, $P = 0.005$) in these gaps at the end of the third year. The *Deschampsia* vegetation gaps had a lower amount of bare ground throughout most of the recording period but after 3 years this was no longer a significant difference.

ANALYSIS OF GAP SIZE, MANAGEMENT TYPE AND SEEDING, BY BLOCK

Gap size

For the blocks at Cavenham (Table 2a, b) there were no significant differences between gap sizes (0.0625 m²–1 m²) for any of the species groups. In the *Calluna* vegetation at Thurstaston (Fig. 3 and Table 2c), bare ground declined faster in the two smallest gap sizes; these gaps also had a higher *Calluna* frequency than in the largest gaps, which was the only significant effect of gap size seen in this

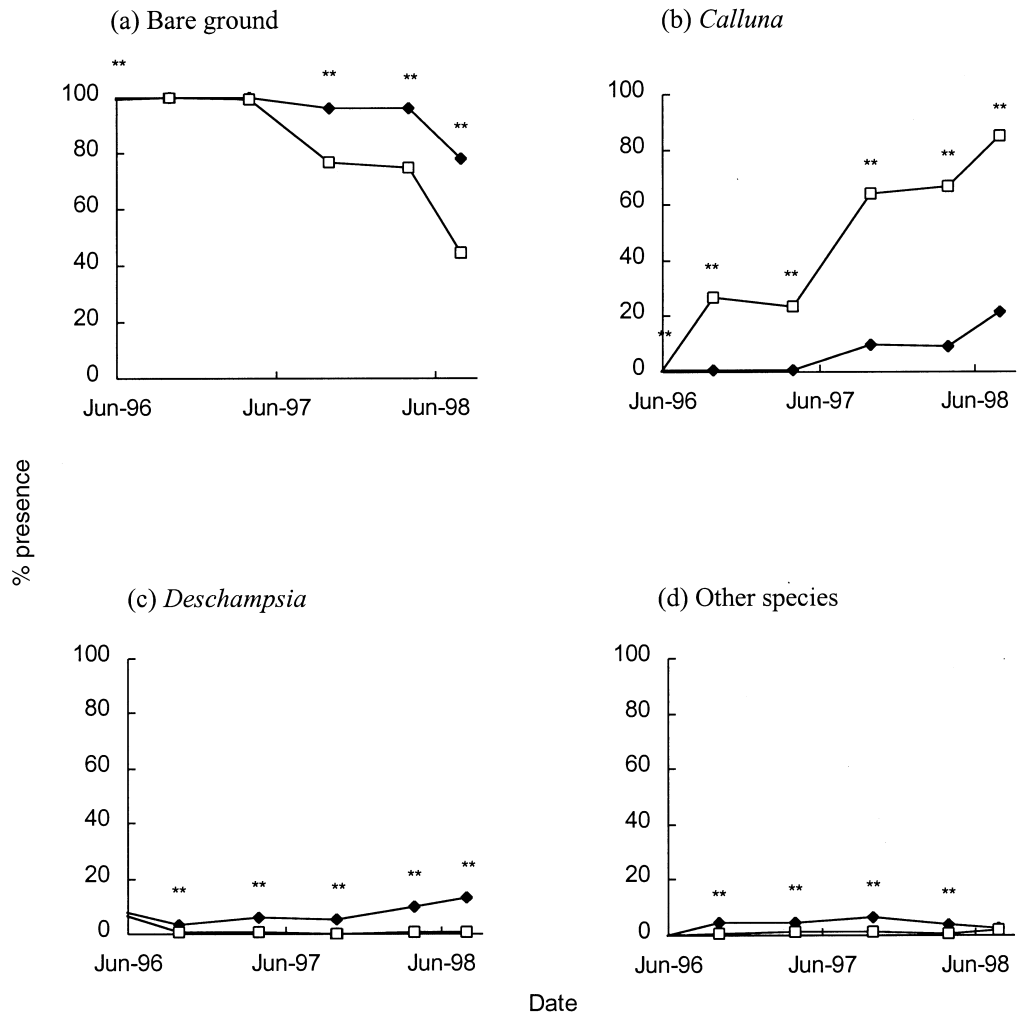


Fig. 1. Vegetation development through time in experimental gaps in *Calluna* stands at Thurstaston Common (Wirral) (open squares) and Cavenham Heath (Suffolk) (solid diamonds). Four species groups are shown. Values are means; ** above a time-point indicates a significant difference between treatments at $P=0.05$.

experiment (Table 2). Frequencies of both *Deschampsia* and 'other' species were very low with no significant differences between gap sizes.

Management type

The *Calluna* block at Cavenham (Table 2a) showed no significant differences between the three management types for the amount of bare ground, *Calluna* or other species. The cutting treatment had a lower *Deschampsia* frequency than the other two treatments in the third year ($F_{2,36}=5.42$, $P=0.0088$) but there was no overall significant difference.

In the *Deschampsia* vegetation at Cavenham (Fig. 4 and Table 2b) the cutting treatment showed a significantly faster reduction of bare ground frequency following treatment than turf-stripped or rotavated gaps, which maintained a high frequency of bare ground for a much longer period. This was the only difference that was significant over the whole time period. None of the gaps showed much development

of *Calluna*, but the gaps created by the cutting treatment had a higher frequency (but not significantly so) of other species than rotavated and turf-stripped gaps. *Deschampsia* frequency appeared to be higher in cut gaps until the beginning of the third year, when the amount of *Deschampsia* in rotavated and stripped gaps increased; but this difference was not significant. There were no significant differences between turf-stripping and rotavating treatments for any of the species groups.

At Thurstaston (Fig. 5 and Table 2c), the cut and turf-stripped gaps showed the fastest revegetation, with rotavated gaps having a significantly higher frequency of bare ground after 3 years. The cut and stripped gaps had a significantly higher frequency of *Calluna* than the rotavated treatment after 2 years, with the stripped gaps showing a rapid increase in frequency during the second year. *Deschampsia* frequency was very low on all treatments, as was the frequency of 'other' species, and showed no significant differences between treatments.

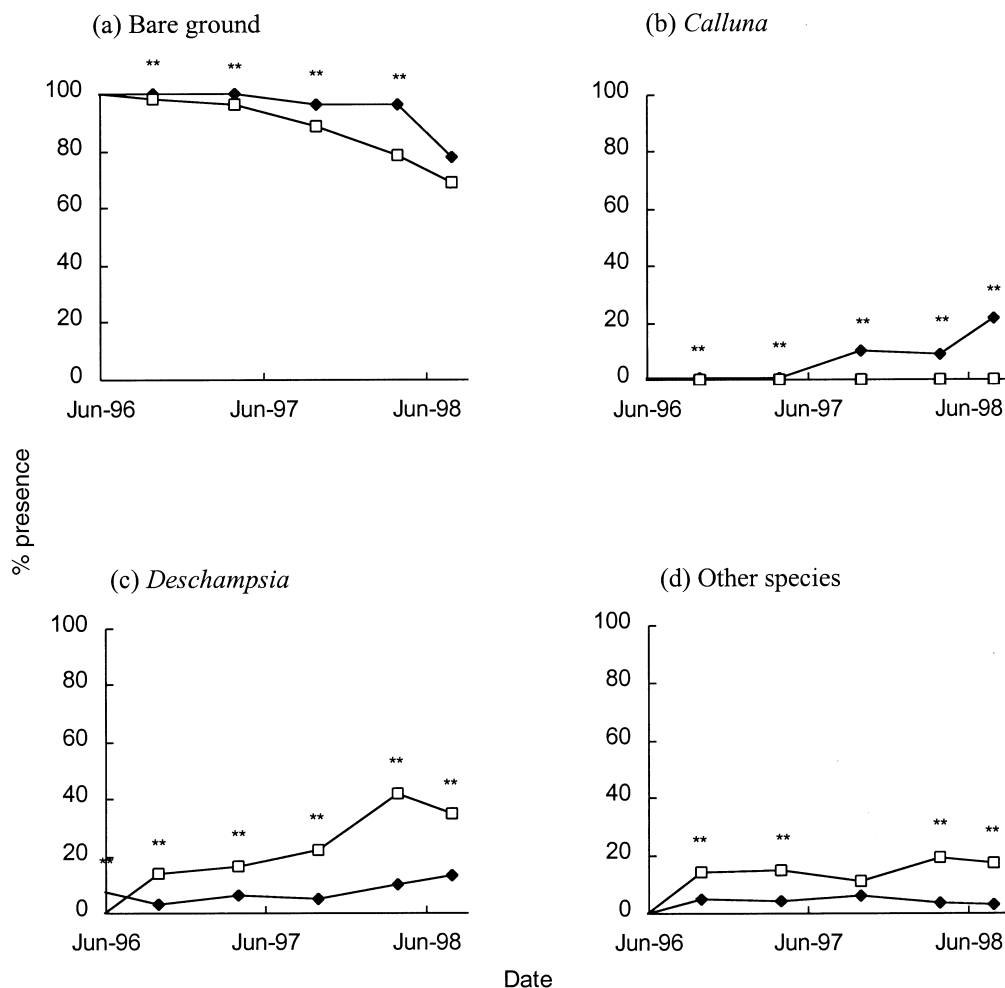


Fig. 2. Vegetation development through time of four species groups in experimental gaps in *Calluna* stands (solid diamonds) and *Deschampsia* stands (open squares) at Cavenham heath (Suffolk). Values are means; ** above a time-point indicates a significant difference between treatments at $P=0.05$.

Seeding

The seeding treatments in the *Calluna* block at Cavenham (Fig. 6 and Table 2a) received *Deschampsia* seed. This had a significant effect on the frequency of *Deschampsia*, which was approximately 30% after 3 years in seeded gaps compared with 3% in unseeded gaps. Seeded gaps also had a significantly lower frequency of bare ground but no significant differences were seen in the frequency of *Calluna* or other species.

Where *Calluna* seed was added to *Deschampsia* vegetation at Cavenham (Table 2b) there was no beneficial effect on the frequency of *Calluna*, which remained very low. The frequency of all the species groups in seeded gaps showed no significant differences from the frequency in unseeded gaps by the end of 3 years.

At Thurstaston, where *Deschampsia* seed was added to *Calluna* (Fig. 7 and Table 2c), the effect on the frequency of *Deschampsia* was small but significant, with higher frequency being seen in seeded

gaps, although this value was still low. *Deschampsia* was the only species group to show sustained significant differences between seeded and unseeded gaps.

Discussion

The comparison of regeneration in *Calluna* stands at Cavenham Heath and Thurstaston Common has shown that there were distinct differences in regeneration dynamics between the two sites. Gaps created in the *Calluna* canopy at Thurstaston were refilled by *Calluna* much more quickly than at Cavenham. In addition, canopy gaps at Cavenham developed a higher *Deschampsia* frequency. In comparing these two geographically separated sites, the effect of a combination of variables is seen. Factors contributing to the difference between sites may include climatic effects, soil properties and nitrogen deposition, the effects of which cannot be separated in this study.

Table 2. *F*-values for treatment effects and interactions in repeated-measures ANOVA for each of the three experimental blocks over the 3-year study period. Only those interaction terms significant for at least one species group are shown. Significance of *F*-values: *** significant at the 0.1% level, ** significant at the 1% level, * significant at the 5% level

Treatment	d.f.	Bare ground	<i>Calluna</i>	<i>Deschampsia</i>	'Other' species
(a) <i>Calluna</i> vegetation at Cavenham heath					
Gap size (G)	2	0.19	1.30	0.27	1.68
Management (M)	2	0.10	0.78	3.12	2.65
Seeding (S)	1	6.77 *	0.07	76.93***	0.00
Time (T)	5	67.81 ***	32.70***	4.91**	9.05***
Error	36				
M × S	2	1.72	0.25	3.42*	0.41
G × M × S	4	1.45	0.80	4.93**	0.33
T × M	10	0.63	0.91	3.09**	0.98
T × G × M	20	1.08	0.52	3.11**	1.31
T × S	5	8.52***	0.27	8.45***	0.27
G × M	4	1.87	0.34	2.56	3.05*
(b) <i>Deschampsia</i> vegetation at Cavenham heath					
Gap size (G)	2	0.87	0.66	1.59	0.14
Management (M)	2	26.30***	1.64	1.84	3.01
Seeding (S)	1	1.29	0.00	0.73	0.10
Time (T)	5	96.19***	4.55**	60.14***	24.33***
Error	36				
T × M	10	9.28***	1.40	2.05*	2.29*
T × G × M	20	0.68	0.33	1.69*	0.84
(c) <i>Calluna</i> vegetation at Thurstaston heath					
Gap size (G)	2	2.18	8.06**	1.91	0.88
Management (M)	2	8.75***	6.82**	2.84	0.75
Seeding (S)	1	3.28	2.23	27.38***	0.02
Time (T)	5	213.24***	473.15***	13.73***	9.42***
Error	36				
G × M	4	6.16***	4.59**	1.32	0.38
M × S	2	4.31*	4.75*	0.33	1.32
G × M × S	4	1.79	3.07*	0.84	0.78
T × G	10	3.74**	4.39***	1.81	2.14*
T × M	10	5.65***	6.49***	0.38	0.64
T × M × G	20	4.02***	2.42**	0.32	0.95
T × M × S	10	2.06	2.34*	2.27	1.30

Pakeman *et al.* (1999) showed that seed bank sizes vary widely between sites with different climates. Samples from Cavenham Heath had a seed bank size only one-quarter of that found at Thurstaston Common. *Calluna* seedlings are also known to be extremely sensitive to drought (Gimingham 1972; Britton 1998), a frequent occurrence in Breckland. High levels of nitrogen deposition have been linked to a reduced ability of *Calluna* to regenerate from cut stems (Berdowski & Siepel 1988), while the growth of grasses, such as *Deschampsia*, may be enhanced (Heil & Diemont 1983; Prins, Berdowski & Latuhihin 1991; Van der Eerden *et al.* 1991). It would seem likely that one or more of these factors interacts to bring about the observed difference between the two sites.

Differences between grass- and *Calluna*-dominated stands at Cavenham were as expected. Gaps in the *Calluna* canopy were mainly refilled with *Calluna* by a mixture of vegetative growth and seedling establishment, while gaps in the *Deschampsia* vegetation

were recolonized by *Deschampsia* seedlings from the seed production of surrounding plants. The amount of available bare ground reduced most rapidly in *Deschampsia* vegetation. Canopy gaps in *Deschampsia* stands appeared to be more easily invaded by other species but the amount of *Calluna* colonizing was very small. Gaps in the *Calluna* canopy were colonized by a small but significant amount of both *Deschampsia* and other species. At Cavenham Heath, the *Calluna* seed bank under *Deschampsia* vegetation appears too small to allow *Calluna* vegetation to regenerate well. This supports the work of Pakeman & Marshall (1997) and Pakeman *et al.* (1999), which showed that Breckland heaths have very small *Calluna* seed banks compared with heaths in other parts of the country.

It was expected that gap size would affect the rate of vegetation regeneration and the number of new species invading, with larger gaps taking longer to regenerate and being more likely to be invaded by new species (MacArthur & Wilson 1967; Denslow

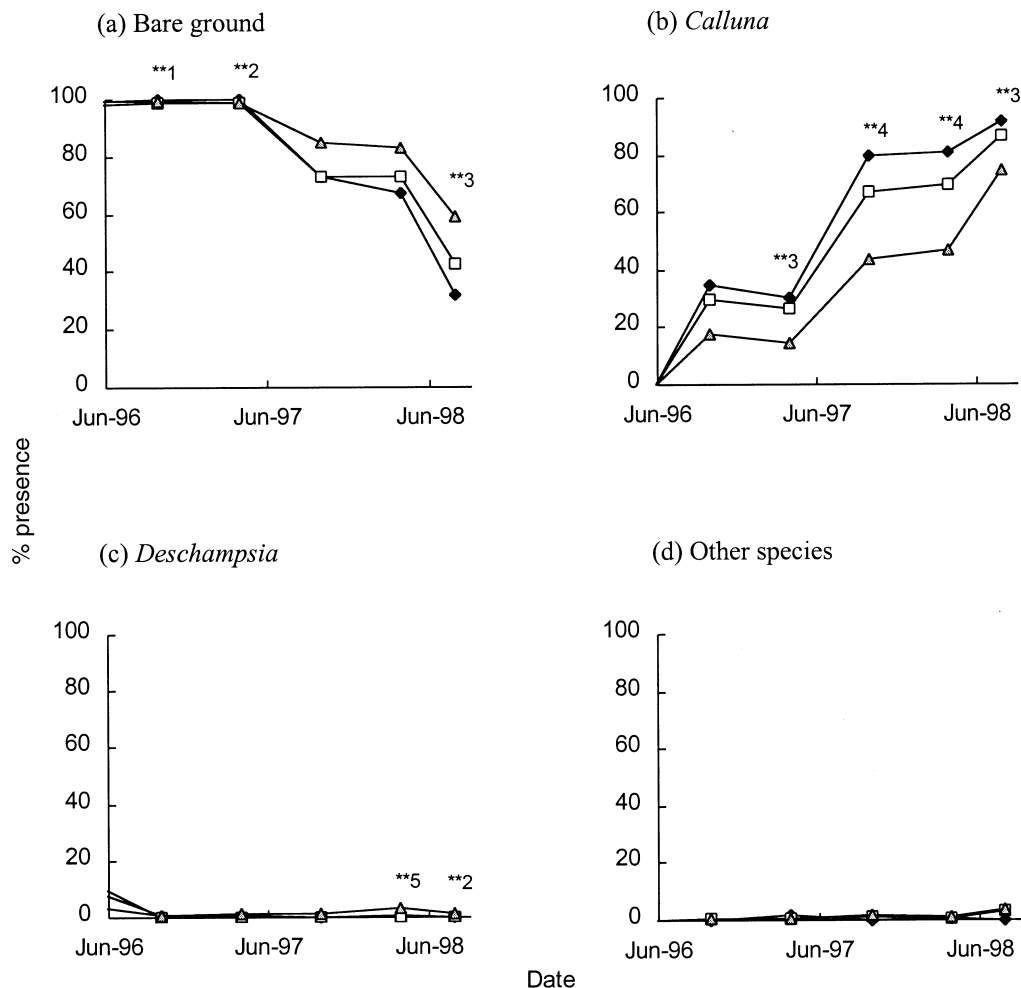


Fig. 3. Vegetation development in gaps of three sizes: 0.0625 m² (solid diamonds), 0.25 m² (open squares) and 1 m² (grey triangles). Results are shown for four species groups in *Calluna*-dominated vegetation type at Thurstaston Common. Values are means; ** above a time-point indicates a significant difference between treatments at $P=0.05$; numbers indicate Bonferroni groupings as follows: 1–0.0625, a; 0.25, b; 1.0, ab; 2–0.0625, a; 0.25, b; 1.0, b; 3–0.0625, a; 0.25, ab; 1.0, b; 4–0.0625, a; 0.25, a; 1.0, b; 5–0.0625, ab; 0.25, b; 1.0, a.

1985). Because large gaps would generally take longer to be filled by expansion of surrounding plants, there should be a longer opportunity for establishment from seed (Bullock *et al.* 1995). However, no significant effects of gap size were found except that *Calluna* refilled small gaps faster at Thurstaston. In *Calluna* vegetation at Cavenham, no effect of gap size was seen and all regeneration was slow. More significant differences might have been seen over an extended recording period or a wider range of gap sizes. In an Australian heath community, Williams (1992) found significant effects of gap size on the outcome of regeneration. Species richness increased with gap size in grassland and open heath communities, possibly due to differences in microclimate and competition between gap sizes. However, this effect was not seen in closed heath communities. Studies of gap recolonization in *Calluna* heath by De Hullu & Gimingham (1984) found that small gaps had a greater number of both emer-

ging and establishing *Calluna* seedlings. In their study, gaps were kept open by removal of regrowth, unlike this study where small gaps were more rapidly filled by vegetative regeneration of surrounding plants. Miles (1974) also found that small gaps had a greater number of germinating seedlings. After 2–3 years, however, this trend was reversed, with survival being lowest in small gaps. It would seem that, while small gaps in closed heath communities may provide a suitable microclimate for germination and seedling survival, they are not conducive to long-term survival of the establishing species. In addition, small gaps may be more quickly closed by lateral growth of surrounding plants when growing conditions are favourable, as at Thurstaston Common.

Cutting or mowing, turf-stripping and rotavating are all used as management practices on British heathlands. Both turf-stripping and rotavating cause significant disturbance to the soil and require plants

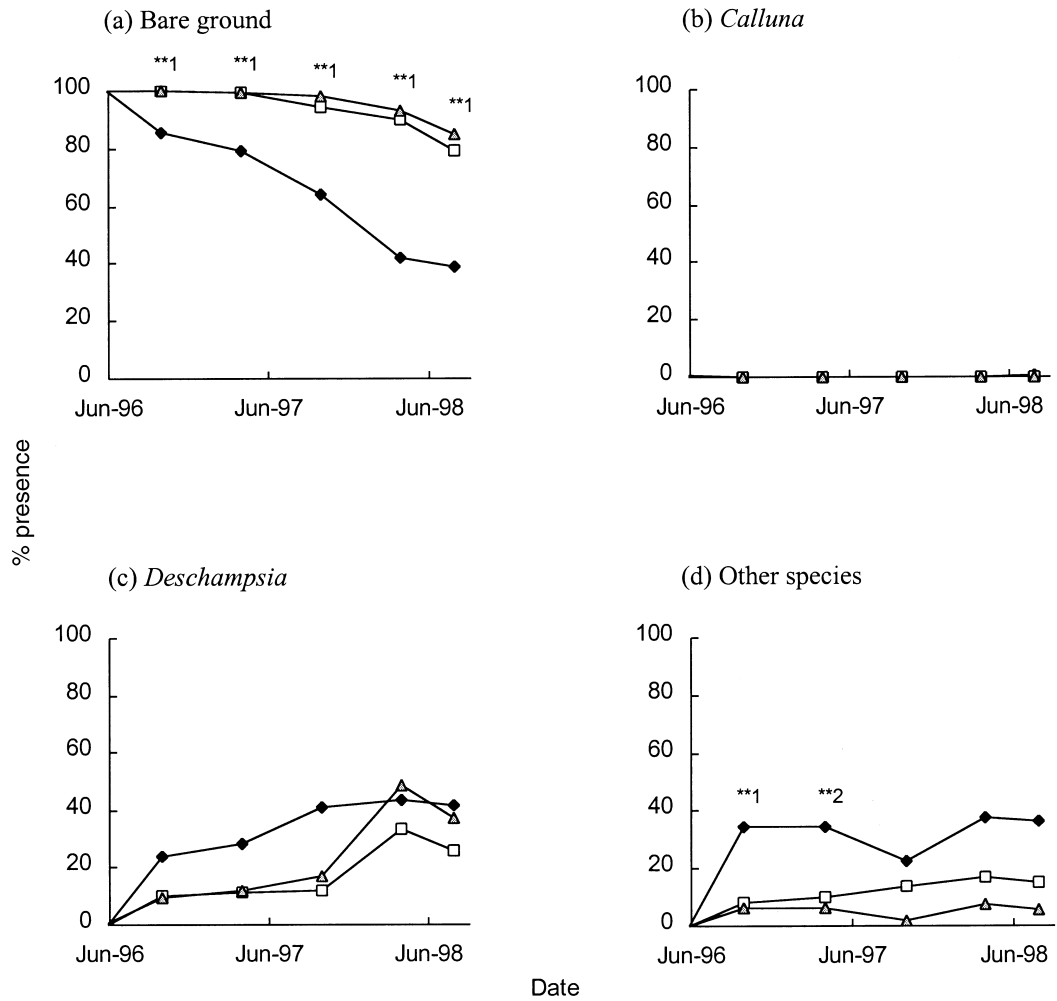


Fig. 4. Vegetation development in gaps created using three management types: cutting (solid diamonds), rotavating (grey triangles) and turf-stripping (open squares). Results are shown for four species groups in *Deschampsia*-dominated vegetation type at Cavenham Heath. Values are means; ** above a time-point indicates a significant difference between treatments at $P=0.05$; numbers indicate Bonferroni groupings as follows: 1, cut a; strip and rotavate, b; 2, cut a; strip, ab; rotavate, b.

establishing in the gaps created to regenerate either from seed or vegetatively from plant parts left at the new surface. Turf-stripping removes soil organic matter, creating low nutrient conditions, which Dutch workers have suggested can favour the establishment of *Calluna* (Diemont & Linthorst Homan 1989; Diemont 1994), while rotavating may result in a pulse of nutrients released from decaying plant parts.

Few significant differences were found between the management treatments in this study. Plot sizes were much smaller than would normally be used for management, with a greater edge: area ratio. This, together with the slow regeneration at Cavenham, may have reduced treatment differences. There was no management type effect in the *Calluna* vegetation at Cavenham. At Thurstaston *Calluna* colonized more quickly in cut- or turf-stripped plots, with recolonization being slower in the rotavated treatment. In *Deschampsia* vegetation, management treatments only had a significant effect on the

amount of bare ground, which remained greater in rotavated or stripped plots. Bare ground should be beneficial to the establishment of *Calluna*, which is negatively affected by shade (Jason & Hester 1993). However, *Calluna* establishment in this block was almost zero, which may be a result of lack of available propagules and poor climatic conditions for establishment of seedlings. Under the hot and dry summer conditions experienced at Cavenham a certain degree of shade from surrounding plants may be beneficial to the survival of *Calluna* seedlings.

Addition of *Calluna* propagules into gaps in the *Deschampsia* vegetation at Cavenham failed to promote the establishment of *Calluna*. The amount of seed applied ($35\,000\text{ seeds m}^{-2}$) may have been too low or conditions not suitable for germination. The seeding rate used was 10 times the normal total seed bank for Breckland heaths (Pakeman & Marshall 1997), and in a heathland restoration trial at the same site Lowday (1984) achieved establishment of

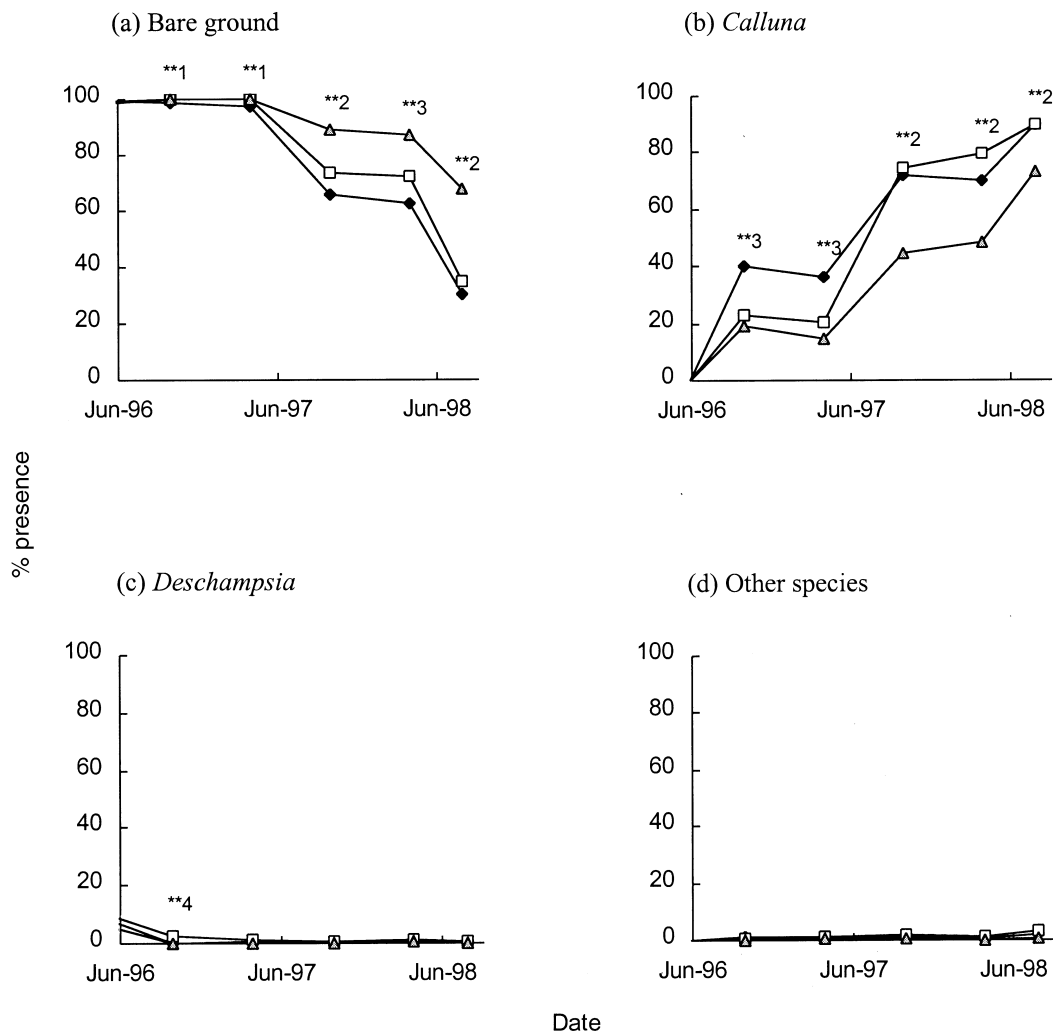


Fig. 5. Vegetation development in gaps created using three management types: cutting (solid diamonds), rotavating (grey triangles) and turf-stripping (open squares). Results are shown for four species groups in *Calluna*-dominated vegetation at Thurstaston Common. Values are means; ** above a time-point indicates a significant difference between treatments at $P = 0.05$; numbers indicate Bonferroni groupings as follows: 1, cut, b; strip and rotavate, a; 2, cut and strip, a; rotavate, b; 3, cut, a; strip, ab; rotavate, b; 4, cut and rotavate, a; strip, b.

10–68% cover of *Calluna* using 20 000 seeds m^{-2} . It therefore seems that lack of establishment rather than lack of seed is likely to be the cause of poor regeneration at Cavenham. The first summer after treatments were applied (1996) was unusually warm and dry in Breckland (M. Wright, personal communication) and few germinating *Calluna* seedlings survived anywhere on the heath. *Deschampsia*, however, which has larger seeds than *Calluna*, is not as sensitive to drought stress (Britton 1998) and was able to establish successfully wherever seed was introduced into the *Calluna* vegetation at Cavenham. This indicates that, at this site, the only factor limiting the spread of this species is the availability of gaps in the *Calluna* canopy and ability of *Deschampsia* seed to reach them. *Deschampsia* does not form a persistent seed bank and seed shed in the autumn germinates directly (Grime, Hodgson &

Hunt 1988). *Deschampsia* also appears to have relatively limited dispersal ability; a range of up to 8 m has been measured by DeSmidt (1985). Thus, establishment of *Deschampsia* requires a population of adult plants nearby. At Thurstaston *Deschampsia* did not establish so well. This may be due to the rapid regrowth of *Calluna*, which refilled the gaps before *Deschampsia* could become established. It would appear that, at this site, *Deschampsia* is unlikely to establish well even where a source of propagules is available.

This work has a number of implications for the management of lowland *Calluna* heath. It was apparent that the response of heathland vegetation to the management treatments applied in this study varied according to site. Slow regeneration of *Calluna* at the Breckland site meant that gaps in the *Calluna* canopy created as a result of management

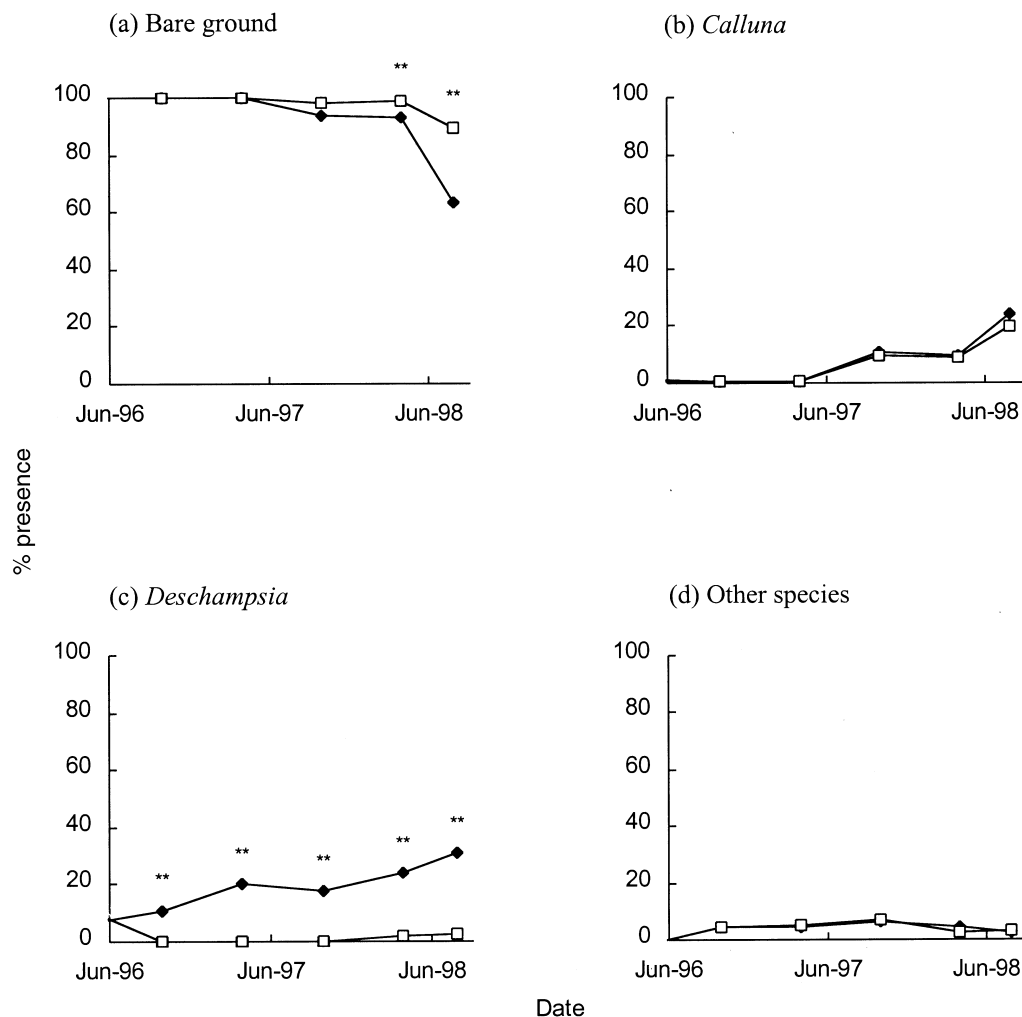


Fig. 6. Vegetation development over a 3-year period in seeded (solid diamonds) and unseeded (open squares) gaps for four species groups in *Calluna*-dominated vegetation at Cavenham Heath. Values are means; ** above a time-point indicates a significant difference between treatments at $P=0.05$.

activities remained open to *Deschampsia* invasion for much longer periods than on the Wirral site. The main limitation to the spread of *Deschampsia* at Cavenham was the ability of propagules to be dispersed into gaps in the *Calluna* canopy. Management activity for *Calluna* regeneration should aim to reduce the probability of this occurring, perhaps by mowing any adjacent areas of *Deschampsia* before seed set, or by use of an appropriate herbicide until *Calluna* has re-established on managed areas.

Use of smaller gaps to encourage faster re-establishment of *Calluna* did not appear to be effective in the short term at these sites, but applying management treatments to smaller blocks may help to spread the risk of the treatment being followed by poor weather conditions for re-establishment. On the north-western heaths, such as Thurstaston, *Deschampsia* invasion is much less of a problem; mowing, rotavating or turf cutting of *Calluna* stands should normally result in re-establishment of *Cal-*

luna. Even where *Deschampsia* propagules are available, however, it appears unlikely that this species will establish to the exclusion of others.

In view of the differences shown here between the regeneration dynamics of these two contrasting sites, it would seem that future prescriptions for management and restoration of lowland heaths should be tailored to fit the conditions prevailing at the individual site, rather than following a standard prescription throughout the UK. The importance of this point must be further emphasized when the variation in species composition associated with different geographical areas is considered. Not all heathlands contain potentially invasive grass species such as *Deschampsia*; for example, the heathlands of the south-west are characterized by *Agrostis curtisii* which is short lived. Such differences increase the variety of response to standard management practices and re-enforce the argument that management must be matched to sites.

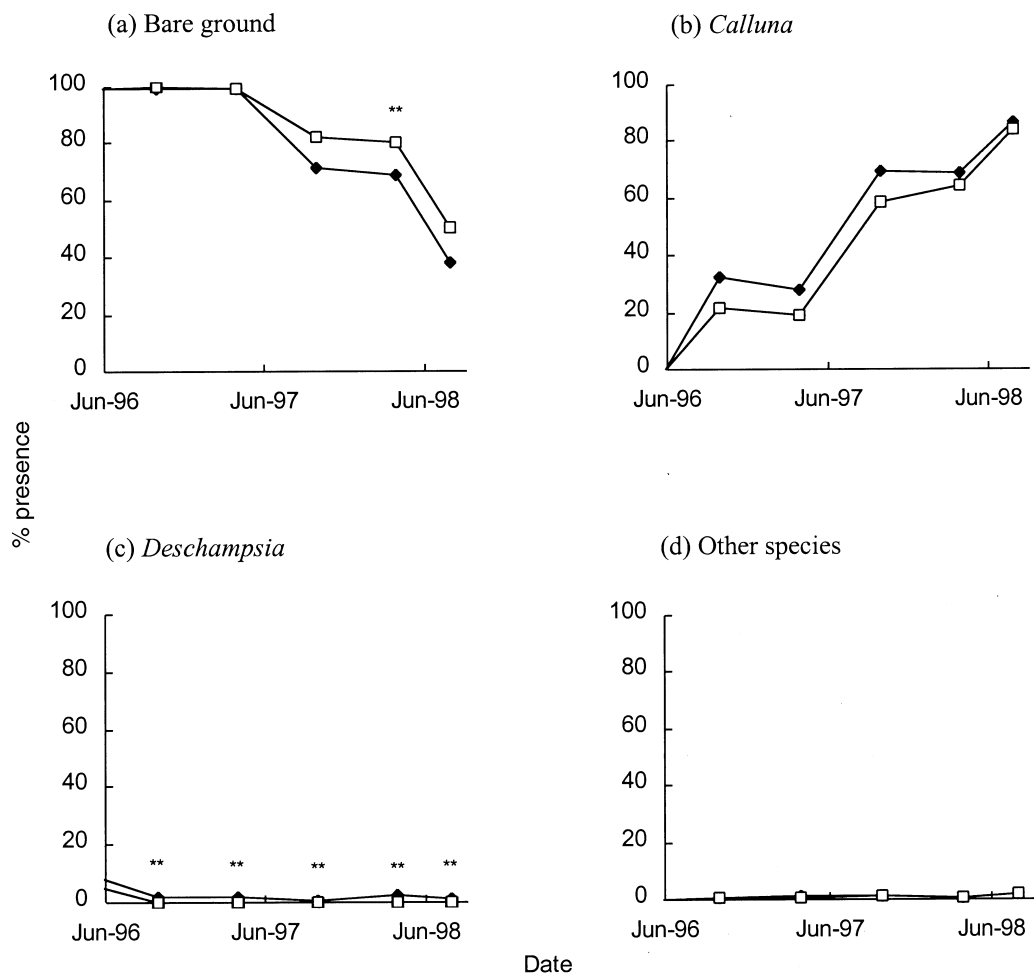


Fig. 7. Vegetation development over a 3-year period in seeded (solid diamonds) and unseeded (open squares) gaps for four species groups in *Calluna*-dominated vegetation at Thurstaston Common. Values are means; ** above a time-point indicates a significant difference between treatments at $P=0.05$.

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References

- Aerts, R., Berendse, F., de Caluwe, H. & Schmitz, M. (1990) Competition in heathland along an experimental gradient of nutrient availability. *Oikos*, **57**, 310–318.
- Bell, N. (1994) *The Ecological Effects of Increased Aerial Deposition of Nitrogen*. British Ecological Society Eco-

logical Issues No. 5. Field Studies Council, Shrewsbury, UK.

- Berdowski, J.J.M. & Siepel, H. (1988) Vegetative regeneration of *Calluna* at different ages and fertilizer levels. *Biological Conservation*, **46**, 85–93.
- Britton, A.J. (1998) Modelling invasions on heathlands. PhD Thesis. University of Liverpool, Liverpool, UK.
- Bullock, J.M., Clear Hill, B., Silvertown, J. & Sutton, M. (1995) Gap colonisation as a source of grassland community change: effects of gap size and grazing on the rate and mode of colonisation by different species. *Oikos*, **72**, 273–282.
- De Hullu, E. & Gimingham, C.H. (1984) Germination and establishment of seedlings in different phases of the *Calluna* life cycle in a Scottish heathland. *Vegetatio*, **58**, 115–121.
- Denslow, J.S. (1985) Disturbance-mediated coexistence of species. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P.S. White), pp. 307–323. Academic Press, San Diego, CA.
- DeSmidt, J.T. (1985) *Zaadverspreiding en zaadvoorraadvorming bij Deschampsia flexuosa en Calluna vulgaris*. The Utrecht Plant Ecology News Report No. 1. Department of Plant Ecology, University of Utrecht, Utrecht, the Netherlands.

- Diemont, W.H. (1994) Effects of removal of organic matter on the productivity of heathlands. *Journal of Vegetation Science*, **5**, 409–414.
- Diemont, W.H. & Linthorst Homan, H.D.M. (1989) Re-establishment of dominance by dwarf shrubs on grass heaths. *Vegetatio*, **85**, 13–19.
- Dolman, P.M. & Sutherland, W.J. (1992) The ecological changes of Breckland grass heaths and the consequences of management. *Journal of Applied Ecology*, **29**, 402–413.
- Farrell, L. (1989) The different types and importance of British heaths. *Botanical Journal of the Linnean Society*, **101**, 291–299.
- Gimingham, C.H. (1972) *Ecology of Heathlands*. Chapman & Hall, London, UK.
- Gimingham, C.H. (1992) *The Lowland Heathland Management Handbook*. English Nature Science, Peterborough, UK.
- Goddard, D. (1999) A study of succession at Thurston Common, Merseyside: changes in vegetation, fertility and soil nutrients. Honours Thesis. University of Liverpool, Liverpool, UK.
- Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology. A Functional Approach to Common British Species*. Unwin Hyman, London, UK.
- Heil, G.W. & Aerts, R. (1993) General introduction. *Heathlands – Pattern and Process in a Changing Environment* (eds R. Aerts & G.W. Heil), pp. 1–24. Kluwer Academic Press, Dordrecht, the Netherlands.
- Heil, G.W. & Diemont, W.H. (1983) Raised nutrient levels turn heathland into grassland. *Vegetatio*, **53**, 113–120.
- Iason, G.R. & Hester, A.J. (1993) The response of heather (*Calluna vulgaris*) to shade and nutrients – predictions of the carbon–nutrient balance hypothesis. *Journal of Ecology*, **81**, 75–80.
- Lowday, J.E. (1984) The restoration of heathland vegetation after control of dense bracken by asulam. *Aspects of Applied Biology*, **5**, 283–290.
- MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Marrs, R.H. (1986) The role of catastrophic death of *Calluna* in heathland dynamics. *Vegetatio*, **66**, 109–115.
- Marrs, R.H. (1993) An assessment of change in *Calluna* heathlands in Breckland, eastern England, between 1983 and 1991. *Biological Conservation*, **65**, 133–139.
- Marrs, R.H., Hicks, M.J. & Fuller, R.M. (1986) Losses of lowland heathland through succession at four sites in Breckland, East Anglia, England. *Biological Conservation*, **36**, 19–38.
- Marrs, R.H., Lowday, J.E., Jarvis, L., Gough, M.W. & Rowland, A.P. (1992) Control of bracken and the restoration of heathland. IV. Effects of bracken control and heathland restoration treatments on nutrient distribution and soil chemistry. *Journal of Applied Ecology*, **29**, 218–225.
- Miles, J. (1974) Effects of experimental interference with stand structure on the establishment of seedlings in Callunetum. *Journal of Ecology*, **62**, 675–687.
- Miles, J. (1988) Vegetation and soil change in the uplands. *Ecological Change in the Uplands* (eds M.B. Usher & D.B.A. Thompson), pp. 57–70. Blackwell Scientific Publications, Oxford, UK.
- Pakeman, R.J. & Marshall, A.G. (1997) The seedbanks of the Breckland heaths and heath grasslands, eastern England, and their relationship to the vegetation and the effects of management. *Journal of Biogeography*, **24**, 375–390.
- Pakeman, R.J., Cummins, R.P., Miller, G.R. & Roy, D.B. (1999) Potential climatic control of seedbank density. *Seed Science Research*, **9**, 101–110.
- Pitcairn, C.E.R., Fowler, D. & Grace, J. (1991) *Changes in Species Composition of Semi-Natural Vegetation Associated with Increase in Atmospheric Inputs of Nitrogen*. NERC Contract Report to NCC. Institute of Terrestrial Ecology, Edinburgh, UK.
- Prins, A.H., Berdowski, J.J.M. & Latuhihin, M.J. (1991) The effect of NH₄ fertilisation on the maintenance of a *Calluna vulgaris* vegetation. *Acta Botanica Neerlandica*, **40**, 269–279.
- Rodwell, J.S. (1991) *British Plant Communities. Vol. 2. Mires and Heaths*. Cambridge University Press, Cambridge, UK.
- SAS Institute Inc. (1988) *SAS/STAT Users' Guide. Release 6.03*. SAS Institute Inc., Cary, NC.
- Stace, C.A. (1991) *New Flora of the British Isles*. Cambridge University Press, Cambridge, UK.
- Trist, P.J.O. (1979) *An Ecological Flora of Breckland*. EP Publishing Limited, Wakefield, UK.
- Van der Eerden, L.J., Dueck, T.A., Berdowski, J.J.M., Greven, H. & Vandobben, H.F. (1991) The influence of NH₃ and (NH₄)₂SO₄ on heathland vegetation. *Acta Botanica Neerlandica*, **40**, 281–296.
- Wallén, C.C. (1970) *World Survey of Climatology. Vol. 5. Climates of Northern and Western Europe*. Elsevier, Amsterdam, the Netherlands.
- Webb, N.R. (1986) *Heathlands – A Natural History of Britain's Lowland Heathlands*. Collins, London, UK.
- Williams, R.J. (1992) Gap dynamics in subalpine heathland and grassland vegetation in south-eastern Australia. *Journal of Ecology*, **80**, 343–352.

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