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Potential climatic control of seedbank density

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Abstract

The relationship between *Calluna vulgaris* seedbank density and climate was investigated using regression analysis and two related techniques (factor-ceiling analysis). The seedbank data originated from published and unpublished studies. Low seedbank densities were associated with sites in the relatively dry, sunny and warm south and east of Great Britain. However, as the climatic variables used in the study were highly intercorrelated, it was not possible to determine which climatic variable had the greatest influence on seedbank density. A hypothesis is described suggesting that the limits of seedbank density can be described for single environmental factors. The operation of other environmental and management factors may reduce the seedbank density to less than this maximum. This is illustrated for a range of climatic variables using factor-ceiling analysis. The processes following seed deposition and the longevity of seeds in the soil are highlighted as possible factors controlled by climate which determine seedbank density.

Keywords: *Calluna vulgaris*, climate, seedbank, factor-ceiling analysis

Introduction

It is well known that environmental factors control plant growth (e.g. Monteith, 1977; Woodward, 1997), and from the agricultural literature in particular, that environmental factors control the production of seed and fruit (e.g. Pigott and Huntley, 1981; Haugh, 1990). However, there is little understanding of how edaphic and climatic conditions affect the development of seedbanks, which are crucial for the regeneration of many species and for the maintenance of species richness in plant communities (Grubb, 1977; Thompson *et al.*, 1997). The exceptions to this are based only on observations of how seedbanks vary across gradients of pH (Pakeman and Marshall, 1997), soil fertility (Kitajima and Tilman, 1996) or across gradients of soil waterlogging (Kirkham and Kent, 1997; Bekker *et al.*, 1998). None of these studies, however, could isolate the effects of the environment on the seedbank from those on the vegetation.

Given the evidence above, as well as more general knowledge of plant population biology, it would not be controversial to suggest that the seedbank of a single species at a single point in space and time is a function of a large number of factors, as well as species-specific traits influencing seed longevity. These could include time since disturbance, previous and present abundance of the species, previous and present fecundity of the species, seed predators and pathogens, edaphic conditions, climate and many more. The seedbank density would also be affected by stochastic events and be subject to measurement error. Unfortunately, it is rare that all this information is measured. However, by examining the relationship between single environmental factors and this seedbank density, some light can be shed on the limiting factors operating in the system. This is shown in Figure 1. If all factors apart from that under study were optimal, then seedbank densities would all coincide with the line labelled ‘environmental limit’, though with some variation as a result of stochastic processes and measurement error. However, as other factors would not always be optimal, then in reality many points would lie below this line. None, of course, could lie above it except as a result of stochasticity and measurement error. The actual test of whether the chosen factor is a limiting factor then rests on whether the slope of the line representing the maximum is significantly different from zero. If not, then variation of that factor, within the measured range, has no role in setting the limit of seedbank density.

This study set out to test whether these limiting factors can be described. The chosen method involved

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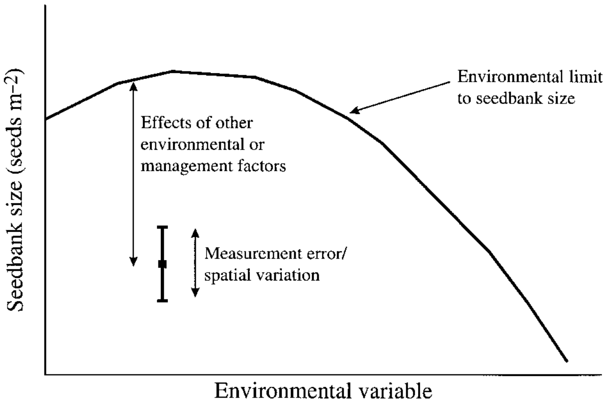

Figure 1. Hypothetical relationship between an environmental variable and seedbank density. The diagram shows the variation as a result of measurement error and spatial variation, the effects of other environmental or management factors in reducing seedbank density and the overall limit set by the controlling factor.

initial selection of factors by traditional regression analysis, followed by the use of two techniques (from a number available) to describe the limits set by the selected factors. The two techniques were ‘edge detection by logistic slices’ (Thomson *et al.*, 1996) and ‘upper bound estimation’ (Blackburn *et al.*, 1992). Alternatives have been presented by Maller *et al.* (1983), Kaiser *et al.* (1994), Thomson *et al.* (1996) and Scharf *et al.* (1998).

To test the possibility that environmental factors control seedbank development a suitable species needed to be investigated. A suitable species would have: (a) a long-lived seedbank which would reduce between-season variability, such that the precise timing of sampling was unimportant; (b) would dominate systems over a long time-scale such that sampling can effectively ignore current abundance and previous site history; and (c) would be a well-studied species so that large quantities of data were available for analysis. Heather (*Calluna vulgaris* (L.) Hull) fitted these criteria. It has long-lived seed, remaining viable in heathland soils for 30–40 years (Gimingham, 1972; Thompson and Band, 1997). It has been shown to persist for more than 60 years (Webb and Pywell, 1992) or even 70 years (Gränstrom, 1988) in soil under coniferous plantations. The half-life of seeds in these plantation soils has been calculated as c. 13 years (Webb and Pywell, 1992). Thus, year-to-year variations in seedbank density will be relatively small, as density is the result of integrating many years of seed production. *C. vulgaris* often forms dense, nearly monospecific stands, such that the seedbank density in these stands will be little affected by variation in plant cover. It is also a well-studied species, as it is important for agricultural and game production, as well as for conservation, so that a considerable amount of data could be drawn from published sources (Table 1).

The dependence of this study on data already collected determined the choice of analysis. As data were collected for a variety of purposes, there were often little associated environmental data collected at the same time. Thus to illustrate the potential control of environmental factors on seedbank density, climatic variables were used because they were available for all sites from currently held databases. Another problem with this approach was the wide variability in techniques used and conditions for germination. Data from studies where heat treatment of soil (> 25°C) had been used were excluded as this enhances the germination of *C. vulgaris* (e.g. Legg *et al.*, 1992). Otherwise, it was assumed that the results from studies where buried seeds were germinated from soil cores of about 50 mm depth in greenhouse conditions were comparable.

Also one proviso must be stated – the analysis does not concern itself with the mechanisms involved. Thus, any patterns shown only demonstrate the potential limit imposed by climatic conditions on the seedbank density of *C. vulgaris*. This control may be a direct function of climatic effects on many processes or it may operate indirectly via control of edaphic factors.

Materials and methods

Published seedbank densities of *C. vulgaris* were collected from as wide a range of sources as possible from within Great Britain (Table 1). Although several samples differed from the desired 50 mm sampling depth, they were kept in the analysis. Much of the seedbank of *C. vulgaris* is concentrated in the soil near the surface so that sampling to a somewhat greater depth than 50 mm will not vary the estimated seedbank density to any great extent (Pywell, 1993).

All the unpublished data were taken from samples of 50 mm depth (Table 2). The English samples were collected in the spring of 1996. Sampling methods and growing conditions were the same as those used by Pakeman and Hay (1996) and Pakeman and Marshall (1997). The Scottish samples were collected over several years but were handled in a consistent manner. The ones used in the analysis represented a subsample of the available data; only sites with a heather cover of 75% or more were selected. Detailed methods are described in Miller and Cummins (1987).

A total of 90 sites from both published and unpublished sources were available for the analysis. Altitudes for the sites were obtained from 1:25 000 or 1:50 000 scale Ordnance Survey maps.

Climate data were derived from the climate LINK project (Viner and Hulme, 1994). This has interpolated

Table 1. Sources of published data of *Calluna vulgaris* seedbank densities

Source	Sites (UK National Grid reference)	Comments
Putwain and Gillham (1990)	Moel Fammau (SJ163607) Denbigh Moors (SH996590) Burbage Moor (SK272807) Fellhouse Fell (NY754590) Lee Moor (SX559629)	
Miles (1973)	Glensaugh (NO655797) Glendye (NO637903) Deskry (NJ403129)	Soil sampled to 20 mm
Pywell (1993)	Grip Heath (SY974885) Hartland Moor (SY950850) Stoborough Heath (SY940856) Arne Heath (SY964887) Horton Common (SU074068) South Heath (SY870887)	Whole depth of soil sampled Top 40 mm contains c. 95% of heather seedbank
Chippindale and Milton (1934)	Ponterwyd (SN7474)	Unknown depth
Mallik *et al.* (1984)	Muir of Dinnet (NO436987)	Two stands sampled, one to 30 mm depth (max. soil depth)
Pakeman and Hay (1996)	Cavenham Heath (TL755725) Levisham Moor (SE836942) Ramsley Moor (SK289760)	
Pakeman and Marshall (1997)	Cavenham Heath, C2 (TL753725) Brettenham Heath, B17 (TL925865) Icklingham Plains, I4 (TL764733) Foxhole Heath, F1 (TL738775)	Data from samples with >75% heather
Pywell et al. (1997b)	Stiperstones (SO364995) Nipstones (SO358969) Heath Mynd (SO334944)	
Mitchell *et al.* (1998)	Arne (SY973882) Avon Heath (SU129035) Blackhill (SY840940) Canford Heath (SZ030995) Cranborne Common (SU104112) Higher Hyde Heath (SY851907) St Catherines Hill / Town Common (SZ142955) Soply and Ramsdown (SZ133974) Trigon (SY884908) Winfrith Heath (SY805865)	Soil sampled to 63 mm
Hester *et al.* (1991)	Tulchan (NJ154373)	

data from the Metorological Office Rainfall and Evaporation Calculation System (MORECS; Thompson *et al.*, 1981) to the 10 km × 10 km squares of the OS National Grid by a partial thin plate spline function. Gridded mean monthly 1961–90 baseline climatologies was available for Great Britain for a number of climate variables at three grid cell elevations (low, mean and high). Elevation data were derived from *A Land Characteristic Data Bank for Great Britain* (Ball *et al.*, 1983). Monthly values for low, mean and high altitudes for the 10 km squares containing our sites were derived for the following climatic variables: mean daily minimum, mean daily and mean daily maximum temperature (°C); precipitation (mm); sunshine hours; relative humidity; wind speed; frost days (defined when grass minimum temperature was below 0°C); rain days (defined when precipitation was greater than 0.2 mm).

The climate data for the maximum, mean and minimum altitudes of each 10 km square were used to produce climatic data for each sample using the altitude of the site and linear interpolation. The data for mean and maximum altitudes were used for the interpolation if the site altitude lay between them, otherwise the mean and minimum altitude data were used.

The climate data for each site were then amalgamated to produce total or mean figures for 3-monthly periods (January–March, April–June, July–September, October–December) in order to reduce the number of climate variables to less than the number of sites (Zar, 1984). Annual figures were also produced for use in separate analyses.

Initial data analysis employed the use of normal multiple, linear regression analysis and stepwise

Table 2. Mean *Calluna vulgaris* seedbank densities (no. m^{-2}) and site locations for unpublished data used in this analysis. All soil sampled to 50 mm depth

Site (grid reference)	Seedbank (no. m^{-2})	Site (grid reference)	Seedbank (no. m^{-2})
Wetherhouse Moor (SE549941)	22 540	Stac na h-lolaire (NJ014083)	47 000
Thurstaton Common (SJ2484)	8490	Glenshee summit (NO138779)	97 000
Minsmere (TM452690)	6590	Carn Crom (NO030952)	38 000
Levisham Moor (SE836942)	33 760	Allt an Eas Mhoir, Ben Avon (NJ142005)	43 000
Ramsley Moor (SK289760)	48 600	Coire Cas, Cairngorm (NH994058)	62 000
Thursley Common (SU908408)	440	Coire Cas, Cairngorm (NH990063)	57 000
Berner’s Heath (TL792764)	640	Glen More (NH985074)	88 000
Horn Heath (TL787775)	580	Glen More (NH984075)	24 000
Weather Heath (TL787777)	2010	Coylumbridge (NH936102)	51 000
Cavenham Heath (TL755725)	2280	Coylumbridge (NH933100)	17 000
Creech Heath (SY9283)	4700	Glenshee summit (NO142776)	17 000
Hartland Moor (SY9485)	4040	Carn Aosda (NO140788)	28 000
Aylesbeare Common (SY0590)	460	Glean Beag, Glenshee (NO133756)	24 000
Roydon Common (TF683227)	759	Glen Clunie (NO145843)	35 000
Coire na Cloiche, Sgòran Dubh Mor (NH882057)	22 000	Muir of Dinnet (NO434985)	58 000
Glen Feshie (NN849965)	96 000	Muir of Dinnet (NO437985)	25 000
Glen Muick (NO322883)	54 000	Meikle Pap (NO258860)	17 000
Carn na Sròine (NJ105202)	85 000	Coire na Ciche, Lochnagar (NO273864)	28 000
Glen Quioch (NO116921)	48 000	Lochnagar (NO275858)	21 000
Glen Clunie (NO151878)	45 000	Glen Muick (NO292860)	31 000
Glenshee summit (NO143776)	41 000	Glen Muick (NO294859)	58 000
Stuc Garb Mhor (NJ148002)	38 000	Cairn o’ Mount (NO651833)	94 000
Glen Luibeg (NO017948)	52 000	Glen Dye (NO649845)	77 000
Glen Feshie (NN876976)	20 000	Conachcraig (NO280866)	12 000
Lochnagar (NO279857)	27 000	Glen Muick (NO283854)	34 000
Lochnagar (NO277859)	32 000	Glen Muick (NO325887)	38 000

regression, with transformation of the data where appropriate. Three separate sets of explanatory variables were used; geographic (Ordnance Survey 1 km grid easting, 1 km grid northing, altitude), quarterly climate data and annual climate data. Selected explanatory variables were then used with techniques more suitable for the description of bivariate distributions (Thomson *et al.*, 1996). Two possible methods of describing bivariate distributions were employed to illustrate the possible existence of a climatic limit on seedbank size.

Method 1 was ‘edge detection by logistic slices’ (Thomson *et al.*, 1996). Data were ranked according to the independent variable and then split into nine groups of 10. These groups were then used to produce presence / absence data for classes of 10 000 seeds. A logistic regression was fitted to this presence / absence data to find the point for each of the nine groups where mostly full classes gave way to mostly empty classes – the inflection point of the logistic curve. These estimated points were then subject to regression analysis in turn using the midpoint of each group as the independent variable.

Method 2 was ‘upper bound estimation’ (Blackburn *et al.*, 1992). However, Blackburn’s technique was modified by splitting the ranked data into groups of equal size (nine groups of 10) rather than equal intervals. The highest value in each of the nine groups was used for regression analysis, using the midpoint of each group as the independent variable.

Results

Northing and easting combined in the same model always gave the best fit to the data in conventional regression analysis (Table 3). This was improved by logarithmic transformation of the seedbank data; a significant model resulted but it explained only 41% of the variation. The inclusion of altitude did not improve the model fits. However, the results show that the seedbank size of *C. vulgaris* is small in the south-east of Great Britain, particularly in Breckland, and increases further north and west (Fig. 2a, b).

Regression models fitted from the climate data always explained slightly less of the variation than the

Table 3. Regression analysis of *Calluna vulgaris* seedbank density (S no. m^{-2}) on geographic and on quarterly and annual climatic variables, showing the best transformed and untransformed models (n = 90)

Explanatory variables	Model	R^2 (%)	F	*P*
Geographic variables				
Easting (*E*), Northing (*N*)	$S = 26\,691 - 54.6E + 38.7N$	36.7	25.2	< 0.001
	$\log_{10}S = 4.79 - 0.0028E + 0.0007N$	41.0	30.2	< 0.001
Quarterly climate data				
Oct–Dec hours of sunshine (H_o)	$S = 77\,378 - 291H_o$	32.2	41.8	< 0.001
Jul–Sep max. temperature (M_J)	$\log_{10}S = 6.73 - 0.158M_J$	38.4	54.8	< 0.001
Annual climate data				
Annual sunshine hours (H_{ann})	$S = 99\,734 - 55.9H_{ann}$	30.2	38.0	< 0.001
Annual rain days (R_{ann})	$\log_{10}S = 2.26 + 0.0087\,R_{ann}$	34.5	46.3	< 0.001

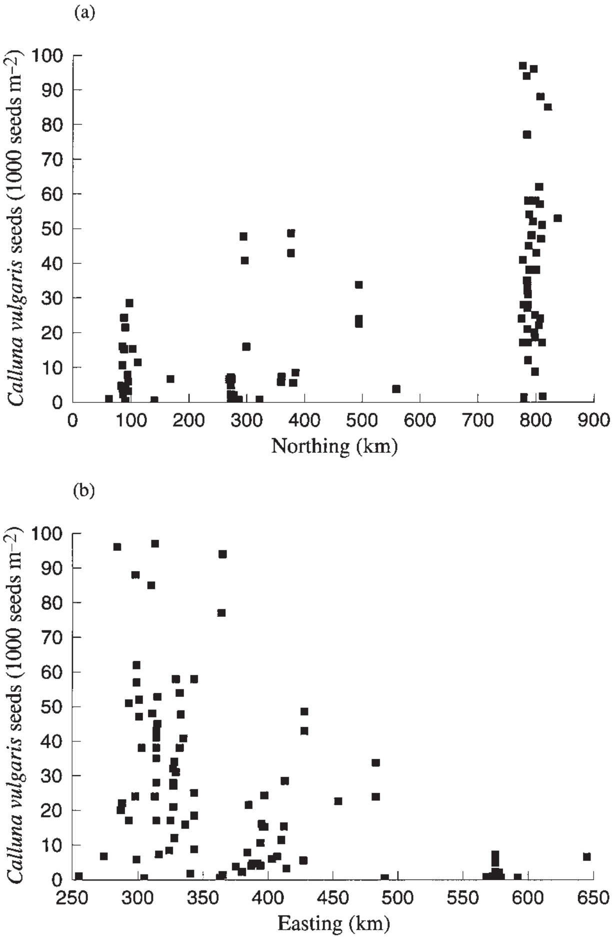

Figure 2. Distribution of *Calluna vulgaris* seedbank density (■) against Ordnance Survey grid (a) northing and (b) easting.

geographic-based models. Fitting the climate data was complicated by the highly intercorrelated nature of the data. For instance, sites which experience high annual temperatures also tend to experience low rainfall, low numbers of rain days, low numbers of frost days and high sunshine hours. Also, quarterly climate data were always highly correlated with the same data from other quarters. Thus the best-fit models were only marginally better than models involving the other climatic variables.

The best-fit model for the untransformed seedbank data was provided by October–December sunshine hours (Fig. 3a, Table 3, R^2 = 32.2%). This was marginally better than models provided by July–September mean temperatures (31.2%), July–September sunshine (31.0%) and October–December mean daily minimum temperatures (30.8%). Logarithmic transformation of seedbank densities increased the percentage of the variation explained. The best-fit model was provided by July–September mean daily maximum temperature (Fig. 3b, R^2 = 38.4%). Other highly significant models were provided by April–June mean daily maximum temperatures (36.8%), July–September mean temperature (36.5%) and October–December sunshine hours (35.9%). No model involving more than one climatic factor significantly improved any of these regression models.

Annual climate data provided different models again. Annual sunshine hours provided the best-fit model of the untransformed data (Table 3, R^2 = 30.2%), closely followed by annual mean temperature (30.0%). Total rain days (34.5%), followed by annual mean temperatures (34.2%), provided the best-fit models of the logarithmically transformed data.

All the best-fit models, and all the other possible models, show that *C. vulgaris* has a smaller seedbank density at sites with higher temperatures, higher sunshine hours, fewer frosts, lower rainfall and a lower frequency of rainfall. The two best-fitting models using the quarterly data, October–December sunshine hours (Fig. 3a) and July–September mean daily maximum temperature (Fig. 3b) are shown for illustration. Fig. 3a shows clearly the large spread of data around the regression lines, the bivariate or

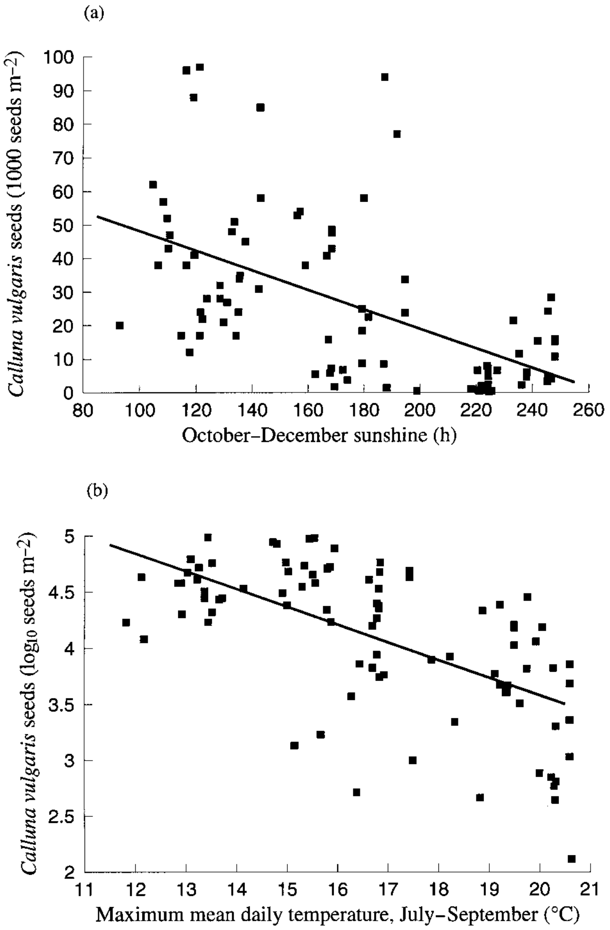

Figure 3. Regression analysis of *Calluna vulgaris* seedbank density (■) against (a) October–December sunshine hours and (b) log transformed seedbank density against July–September maximum mean daily temperature (°C).

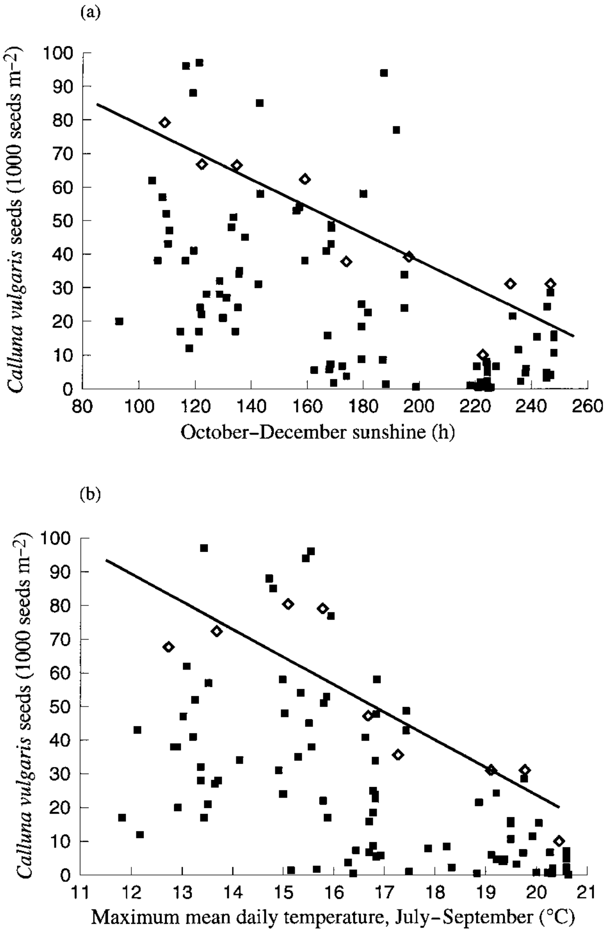

Figure 4. Regression analysis of inflection points (◇) from logistic slicing relating limiting *Calluna vulgaris* seedbank density to (a) October–December sunshine hours and (b) July–September maximum mean daily temperature (°C). Original data shown as (■).

'triangular' spread of data (Maller *et al.*, 1983) and hence the utility of using some form of factor-ceiling analysis.

For illustration these two datasets in Figure 3 were chosen for further analysis. However, the log-transformed data did not prove amenable to the chosen techniques, normally distributed data were not necessary for the assumptions of the techniques, and hence the untransformed seedbank data were used in all subsequent analyses. Using the method of Thomson *et al.* (1996) to fit logistic slices, the inflection points were calculated and are shown in Figures 4a and b respectively. This was not possible for the highest temperature group and third highest sunshine group, as only one class of seedbank size was present. The midpoint of this class was used in the analysis. The regression lines through these inflection points produce a good fit with more than 75% of the variation explained (Table 4), and both slopes were significantly different ($P < 0.05$) from zero. In both cases a linear regression provided the best fit, though there was a suggestion that with more data from colder sites a polynomial may have provided a better fit for the July–September mean daily maximum temperature data. Similarly, a good fit was achieved using the maximum of each class (Blackburn *et al.*, 1992) as shown in Figures 5a and b. Again, linear regression provided the best model, though again a polynomial might provide a better fit for the July–September mean daily maximum temperature data if there were more data from sites with lower temperatures. Both slopes were significantly different from zero.

The linear models relating October–December sunshine hours to *C. vulgaris* seedbank density (Figs. 4a and 5a) suggest that over the range of data

Table 4. Regression results from factor-ceiling analysis of *Calluna vulgaris* seedbank data (n = 9) following the methods of Thomson *et al.* (1996) and Blackburn *et al.* (1992)

Explanatory variables	Model	R^2 (%)	F	*P*
Logistic slices				
Oct–Dec hours of sunshine (H_o)	$S_{max} = 119\,310 - 407.2H_o$	81.7	31.4	< 0.001
Jul–Sep max. temperature (M_J)	$S_{max} = 187\,861 - 8212\,M_J$	76.4	22.6	0.002
Maximum data per slice				
Oct–Dec hours of sunshine (H_o)	$S_{max} = 153\,420 - 527.1H_o$	57.3	9.41	0.018
Jul–Sep max. temperature (M_J)	$S_{max} = 226\,308 - 10\,155\,M_J$	65.4	13.2	0.008

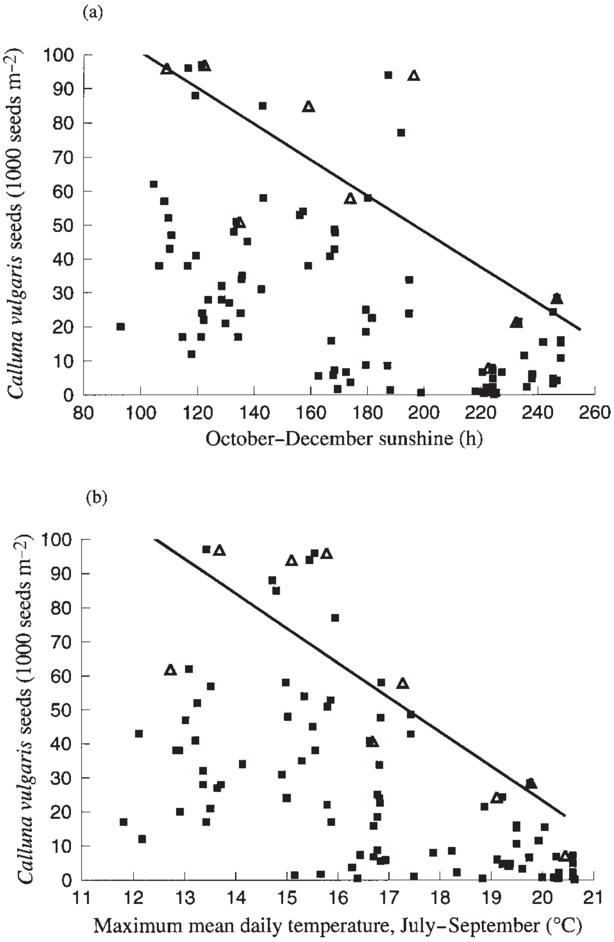

Figure 5. Regression analysis of maximum data from each environmental class (△) of *Calluna vulgaris* seedbank density to (a) October–December sunshine hours and (b) July–September maximum mean daily temperature (°C). Original data shown as (■).

available a high total of sunshine hours would predict a lower maximum seedbank density. The models relating July–September mean daily maximum temperature to *C. vulgaris* seedbank density (Figs. 4b and 5b) suggest a similar relationship – high summer temperatures prevent the development of a high seedbank density. However, the possibility of a significant quadratic model suggests that very low temperatures could also prevent the development of a high seedbank density.

Discussion

Data sources and methodological problems

In analyses of this type, it must be borne in mind that considerable methodological differences exist between the various sources of data. However, all the seedbank data were derived from sites where heather was the dominant species, usually in the mature phase. This should reduce the possible variability associated with heather stand age and the actual amount of heather present in the vegetation. In addition, all data were from soil emergence tests, such that the differences attributable to the use of different techniques (e.g. flotation or elutriation) were absent (Gross, 1990; Warr *et al.*, 1993). Despite the same method being used, there was a great potential for differences in actual growing conditions used by investigators and between years in the same experimental set-up. However, the edge-detection techniques used were concerned only with the edge of the distribution, and thus underestimates of germinable seed density in some samples would not contribute significantly to the analysis.

One obvious difference between the various sampling methods used was the actual depth of soil sampled. However, as the majority of seeds are present in the surface layers (Putwain and Gillham, 1990; Pywell, 1993) the effects of these differences in sampling depth should be relatively small. In the four heathland sites sampled by Pywell *et al.* (1997a), 95% of *C. vulgaris* seed occurred in the top 40 mm of soil. Thus only the three sites sampled by Miles (1973) may have provided substantial underestimates of the actual total seedbank, as only the top 20 mm of soil was removed. The removal of these data from the analysis increased the fit of the simple regression models, especially the easting and northing models (linear data $R^2 = 42.8$, log transformed data $R^2 = 51.8$) and the model with July–September mean daily maximum temperature (log transformed data $R^2 = 45.6$). However, their effect on the other analyses was minimal, as these were designed to detect the upper limits of the data.

The results obtained from the analysis of the data may have been somewhat restrained by the distribution of the sampled sites. Few sites from the extreme west of Great Britain were sampled, though the east–west distribution of the other sites reflects the east–west distribution of land in Great Britain (Fig. 2). There was also a concentration of data from the Cairngorms and surrounding mountains, and very little from southern or northern Scotland. However, sites were evenly distributed in relation to altitude, except for a concentration of sites from southern England below 100 m. However, the use of climate data for the analysis provided a more evenly distributed data set for the regression analysis (*cf.* Figs. 2 and 3). It should also be noted that the use of each site's actual, if it were known, rather than interpolated climate could have further increased the percentage of the variance explained by the models.

Climatic control of seedbank density

The results of the regression analysis and the data shown in Figures 2 and 3 suggest that *C. vulgaris* seedbank density is well correlated with climate. As the climatic data for Great Britain used in this analysis are highly intercorrelated, no one climatic factor can be pinpointed as the primary controlling factor governing seedbank density. It is clear, though, that generally sites in the drier, warmer, sunnier south and east of Great Britain have smaller seedbanks than sites from the north and west.

However, all the linear and transformed regression relationships explained only a relatively small, though significant, part of the variation in the data. Many factors may contribute to the variation in seedbank density, but as already stated, environmental conditions may set the limit to this density. Therefore several techniques were used to describe the relationship between two climate variables selected by regression analysis and the limits of *C. vulgaris* seedbank density, with the assumption that the edges of a 'point cloud' are ecologically informative (Figs. 4 and 5).

The logistic slicing technique described by Thomson *et al.* (1996) showed that both the chosen climate variables, October–December sunshine and July–September mean daily maximum temperatures, were well correlated with the 'ceiling' of the data (Fig. 4). That is, high sunshine or high temperatures are negatively correlated with maximum seedbank size. The dataset chosen has an advantage over that collected by Thomson *et al.* (1996) in that it was more evenly distributed along the axes of the independent variables, and hence the trends were more evident. However, the relatively low number of data points meant that in some instances it was not possible to always provide a good estimate of the inflection point of the logistic curve (i.e. around 220 h of sunshine and 20.5°C).

The method devised by Blackburn *et al.* (1992) picked up a similar significant relationship between the limit of the 'point cloud' and the chosen climate variables (Fig. 5). However, the models described by this method do not fit as well as those provided by the logistic slicing technique (Table 4). The latter technique is less influenced by outliers in the data, and hence potentially more robust.

Ecological and conservation significance

The relationships highlighted here suggest that there is an upper bound on the density of the seedbank of *C. vulgaris* that is related to climate. However, seedbank density is the integral of a number of processes, from flower production, seed set and seed dispersal through to seed incorporation into the soil and its subsequent longevity. Evidence for variation of flower production and seed set across Great Britain is equivocal. Two studies from one site in Scotland (Mallik *et al.*, 1984; Barclay-Estrup and Gimingham, 1994) have similar figures for *C. vulgaris* seed shed, 183 000 and 198 580 m^{-2} respectively, to that of a study from Dorset which showed a seed shed of 168 000 m^{-2} (Pywell *et al.*, 1995). All three figures were estimated from stands of mature heather with c. 100% cover. However, colder, wetter climates may actually reduce flowering and seed set (Miller and Cummins, 1987), and year to year variation in seed set can be considerable (Hester, 1988). Seed dispersal should not contribute to the variation, as all samples were from within stands of mature heather, where the reduction in seed rain as a consequence of dispersal out of the stand would have been negligible anywhere away from the stand edges.

In consequence it is quite possible that post-dispersal processes are of most importance in governing seedbank size in *C. vulgaris*. These processes are seed germination, seed incorporation into the soil and seed survival in the soil. Seed germination may be restricted under a dense heather canopy and many seeds may not be immediately germinable (Putwain and Rae, 1988). Seed incorporation into the soil or seed survival in the soil may both be affected by climatic conditions, the nature of the soil or the soil flora and fauna present (Miller and Cummins, 1987), or a combination of both. However, it is not possible to suggest which of these three processes is the major determinant of seedbank build-up. A possible reason for the absence of altitude in the regression models, and the existence of a possible quadratic relationship between seedbank size and temperature, can be explained by the interaction of two opposing mechanisms. Cold summer temperatures may limit seed-set, possibly via an inhibition of pollinator activity, and cold temperatures appear to inhibit germination and the activities of fungal pathogens (Miller and Cummins, 1987). The possibility of a quadratic relationship is further strengthened by data from Shetland (23 897 seeds m^{-2}, Nolan *et al.*, 1998) and from Fair Isle (12 675 seeds m^{-2}, Nolan *et al.*, 1994), which suggest that seedbank size may be smaller at sites with low summer temperatures (c. 10°C and 11.9°C at the Shetland and Fair Isle sites respectively).

The data revealed a pattern that may be of management and conservation importance. They confirm previous observations (Pakeman and Hay, 1996; Pakeman and Marshall, 1997) of the low density of germinable *C. vulgaris* seeds in southern, lowland heaths in comparison to those from northern heaths and moorlands. In the short-term this means that management (e.g. burning) and restoration methods developed on northern heather-dominated communities need careful consideration before their employment on southern heathlands, where the smaller seedbank resource may imply a reduced resilience within the heathland system. In addition, heather in northern communities has the added advantage over plants in southern, dry systems in that it can regenerate by layering as well as by seed (Scandrett and Gimingham, 1989; Macdonald *et al.*, 1995). In the longer term, the consequences of human-induced changes in global climate could affect the long-term survival of southern heaths. If the climate of these southern heaths becomes drier and warmer as a result of these changes, then this might restrict seedbank build up as well as the probability of successful regeneration after disturbance through reduced seedling survival (Marrs, 1993; Pakeman and Marshall, 1997).

One further conclusion from the exploratory analysis is that experimental investigations are necessary to elucidate which processes involved in seedbank dynamics are influenced by climate and other environmental conditions, and whether these factors actually influence seedbank density. Understanding this would contribute considerably to understanding the population dynamics of species where regeneration from the seedbank is crucial.

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