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Seed production and population density decline approaching the range-edge of *Cirsium* species

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Summary

- Patterns in population density and abundance, community composition, seed production and morphological traits were assessed across the UK geographical range of *Cirsium acaule*, *Cirsium heterophyllum* and *Cirsium arvense* based on the expectation that environmental favourability declines from core to periphery of a species range.
- These traits were measured in natural populations along a latitudinal transect in the UK and using botanical survey data.
- A significant decline in population density and seed production occurs approaching the range edges of *C. acaule* and *C. heterophyllum*. There is no latitudinal trend in these traits in the widespread *C. arvense* and no latitudinal pattern to variation in morphological traits or community composition in any of these species.
- Although seed production is reduced at the range edge of *C. acaule* and *C. heterophyllum*, peripheral populations of these species may persist through clonal reproduction. Low seed production may interact with reduced availability of favourable habitat to limit range expansion in these species.

Key words: *Cirsium*, seed production, geographical range, latitudinal gradient, population density, quantitative trait, morphology, clonal reproduction.

Introduction

Species' range boundaries often show a close association with particular climatic variables (Pigott, 1968, 1992; Conolly & Dahl, 1970; Tofts, 1999). This observation is supported by both correlative approaches linking distributional limits with isometric lines of climate (for example; Salisbury, 1926, Conolly & Dahl, 1970) and identification of the principal factors that limit the spread of particular species (Pigott, 1968; Pigott & Huntley, 1981). Low temperatures may limit poleward spread through their actions on both the vegetative (Woodward, 1990, 1997) and reproductive phases of plant growth (Pigott, 1968; Pigott & Huntley, 1981; Woodward, 1990). The factors limiting spread in the equatorial direction are less clear. High temperature (Conolly & Dahl, 1970) and water availability (Pigott & Pigott, 1993) have been implicated and competitive exclusion may play a key role (Woodward, 1996).

The favourability of a species' environment is expected to decline from the core to the periphery of a species' range (Brown, 1984), based on the observation that environmental factors frequently change in a clinal manner (Endler, 1977). This pattern is expected to result in a decline in the favourability of a species' typical habitat toward the range edge and, consequently, a reduction both in the abundance of individuals within a population and the density of populations within an area (Hengeveld & Haeck, 1982; Brown, 1984). Habitat at the geographical range margins is expected to be ecologically marginal for many species (Lawton, 1993, Lesica & Allendorf, 1995). This is predicted to result in a species occurring in atypical habitat (and hence different plant communities; Crozier & Boerner, 1984; Dibble *et al.*, 1999) in peripheral areas, where the impact of decreased environmental favourability is reduced (Lesica & Allendorf, 1995). Declining environmental favourability is expected to result in a decrease of both plant growth and reproduction toward species' range boundaries (Parsons, 1991).

Many species exhibit a decline in seed production toward their range boundary (Pigott, 1968; Pigott & Huntley, 1981; Reinartz, 1984b; Eckert & Barrett, 1993; García *et al.*, 2000; Dorken & Eckert, 2001). The reproductive phase of the plant lifecycle shows particular sensitivity to climate (Marshall, 1968; Pigott, 1968; Pigott & Huntley, 1981; Houle & Filion, 1993; Despland & Houle, 1997; Woodward, 1997; García *et al.*, 2000). Variation in vegetative characters such as plant size (Marshall, 1968; Clevering *et al.*, 2001) and differential allocation to above- and below-ground organs (Benowicz *et al.*, 2000) toward a species' range limit have also been reported. Differences in plant size may ultimately be reflected in the reproductive success of the plant (Reinartz, 1984a,b; Primack, 1987; Wesselingh *et al.*, 1997).

Many studies have reported variation in plant characters along altitudinal or latitudinal gradients (Clausen *et al.*, 1940; Pigott, 1968; Lacey, 1984; 1988; Aizen & Woodcock, 1992; Winn & Gross, 1993; Wesselingh *et al.*, 1994; Jonas & Geber, 1999). Although investigation into the effects of reaching a species periphery is often inherent in studies conducted over latitudinal gradients, there is a bias toward investigating the poleward periphery of a species distribution. Studies that record trait variation toward the equatorial periphery or across the entire geographical range of a species are relatively rare (but see Reinartz, 1984a,b; García *et al.*, 2000). Furthermore, studies usually concentrate on a few closely related traits and can therefore present only a fragmented view of plant performance across a species geographical range. Seed production, for example, may represent an integrated measure of plant productivity. A reduction in seed production may result from a specific physiological limitation on seed development (Pigott & Huntley, 1981), or an overall reduction in plant growth (Reinartz, 1984a,b; Primack, 1987). This study aims to present a more extensive view of variation in plant traits from the core to the periphery of a species' range.

We report trait variation across the UK geographical range of three *Cirsium* species (*C. acaule*, *C. arvense* and *C. heterophyllum*, Fig. 1). These are perennial, insect-pollinated species that produce wind-dispersed seeds. In addition to reproduction by seed, all reproduce vegetatively by the production of new shoots from underground root and stem tissue (Pigott, 1968; Moore, 1975; Clapham *et al.*, 1981; Grime *et al.*, 1989). *Cirsium acaule* reaches a northern distributional limit in the UK, in Europe it extends from northern England and Estonia southwards to southern Spain, Serbia and south-east Russia (Tutin *et al.*, 1976). *Cirsium heterophyllum* occurs at low altitudes in northern Europe and the eastern part of the former USSR, and reaches a southern distributional limit in the UK (Fig. 1). High altitude populations of *C. heterophyllum* occur in the mountain ranges of Europe, southwards to the Pyrenees and Transylvania (Tutin *et al.*, 1976). *Cirsium arvense* is a widespread species used for comparison. It occurs almost throughout Europe and is absent only from Svalbard in the extreme north and Crete and the Azores in the south (Tutin *et al.*, 1976). Previous studies have reported a close association between both the northern range boundary of *C. acaule* and the southern boundary of *C. heterophyllum* with isotherms of summer temperature (Pigott, 1968; Conolly & Dahl, 1970), implicating climate as a major factor in determining the distribution of these species.

This work will build on previous studies that report geographical patterns in single traits within single species. It will allow both interspecific and intraspecific comparison of trait patterns by reporting intraspecific geographical variation in key areas of population distribution, community composition, morphology and seed production within three congeneric species. A companion paper (Jump *et al.*, 2003) will presents geographical patterns in the population genetic structure of these species.

Given the predicted decline in environmental favourability, this study aims to determine whether gradients in morphological characters, seed production, population density and abundance occur from the core to the periphery of *C. acaule* and *C. heterophyllum* in the UK and whether geographically peripheral populations of these species occur in atypical plant communities.

Materials and Methods

As this work will investigate potential north–south clines in characters in these species, latitude will be used as a proxy for distance from the core of the species distribution. Latitude is a good proxy for the action of many factors such as radiation balance, length of growing season and the frequency of frost events. Indeed, Valentini *et al.* (2000) reported latitude to be a better correlate of ecosystem respiration than any single factor they tested (including mean annual temperature, precipitation and elevation) when investigating forest carbon balance. Furthermore, investigating core–periphery patterns in species has the inherent problem that range edges are extremely difficult to define reliably (Blackburn *et al.*, 1999). Thus, when investigating north–south clines, latitude is a surrogate measure that provides both an indication of the position of populations and the distance between them in the absence of a reliable and repeatable method of defining a species range edge.

Surveys were carried out during July and August 2000 within the populations listed in Table 1. *Cirsium acaule* populations were surveyed only on slopes facing south to south-east since Pigott (1968) reported great sensitivity of seed production to aspect in this species. In this species, comparing data from sites of different aspect could potentially obscure any latitudinal pattern that may occur within similar populations. Populations of *C. heterophyllum* and *C. arvense* were surveyed on level ground.

Population density

Population density was determined by comparing the 2 × 2 km (tetrad) Botanical Society of the British Isles (BSBI) Monitoring Scheme survey data with the 10 × 10 km (hectad) survey data of the Atlas of Flowering Plants and Ferns of Britain and Ireland (Preston *et al.*, 2002). The BSBI

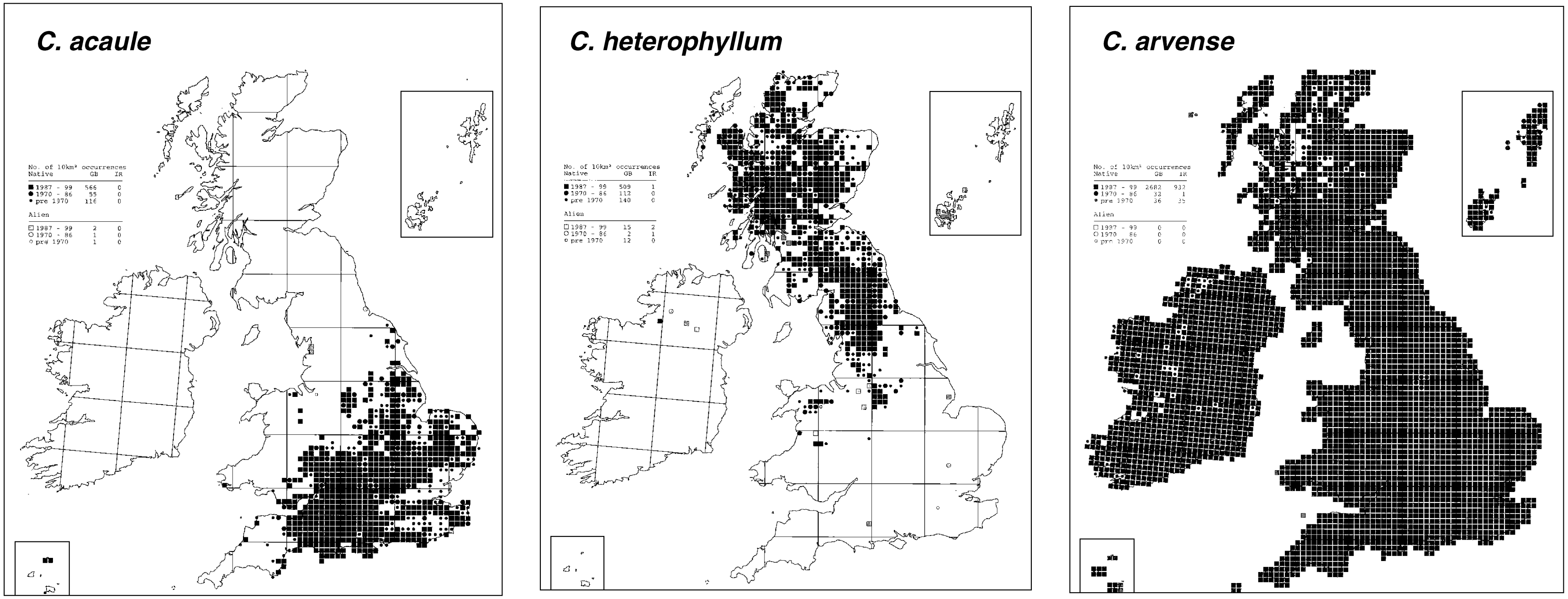

Fig. 1 Distribution maps showing the presence of *Cirsium* species in 10 km squares in Britain and Ireland. Reproduced from Preston *et al.* (2002) with permission.

Table 1 Location of study populations

Cirsium acaule			*Cirsium heterophyllum*			*Cirsium arvense*		
Site code	Site location	Altitude (m)	Site code	Site location	Altitude (m)	Site code	Site location	Altitude (m)
11	50.587°N 2.032°W	70	51	53.214°N 1.765°W	280	11	50.677°N 2.644°W	130
12	50.672°N 2.587°W	150	52	53.231°N 1.844°W	320	12	50.684°N 2.655°W	140
13	50.630°N 1.969°W	80	53	53.241°N 1.780°W	290	31	51.439°N 2.401°W	180
21	51.209°N 2.092°W	130	54	53.166°N 1.879°W	270	32	51.430°N 2.404°W	230
22	51.262°N 2.034°W	160	61	54.408°N 2.337°W	220	41	51.839°N 2.107°W	170
23	51.269°N 2.023°W	130	62	54.439°N 2.587°W	170	42	51.862°N 2.071°W	260
31	51.447°N 2.401°W	180	63	54.862°N 2.508°W	200	51	53.214°N 1.765°W	280
32	51.430°N 2.404°W	230	64	54.447°N 2.387°W	270	52	53.145°N 1.728°W	260
33	51.327°N 2.791°W	150	71	56.490°N 4.748°W	200	61	54.521°N 2.497°W	200
41	51.842°N 2.107°W	190	72	56.400°N 5.213°W	80	62	54.527°N 2.329°W	160
42	51.865°N 2.073°W	260	73	56.321°N 3.685°W	100	71	57.321°N 4.363°W	240
43	51.842°N 1.996°W	210	81	57.101°N 3.987°W	260	72	57.101°N 3.987°W	260
51	53.262°N 1.733°W	320	82	57.015°N 4.162°W	290			
52	53.138°N 1.714°W	250	83	57.327°N 3.021°W	320			
			84	57.420°N 2.627°W	230			
			91	57.990°N 4.814°W	150			
			92	58.243°N 5.177°W	50			
			93	57.753°N 5.011°W	200			

Monitoring Scheme survey is a systematic survey that takes up to three tetrad subsamples from one in every nine (11%) of the hectads of the BSBI grid (see Rich & Woodruff, 1990, 1996). Since, from the Atlas survey, we know whether the species of interest occurs in the hectad being sampled, the density of populations of that species within that hectad is indicated by the number of tetrad samples of the monitoring scheme survey that record it. Thus, a decline in population frequency will be represented by a decline in the number of tetrads per hectad that include the species of interest.

A frequency score was calculated by dividing the number of tetrads per hectad containing the species of interest by the number of tetrad samples taken within that hectad. As tetrad samples have been taken only within hectads where the species of interest is known to occur, a score of 0 indicates lowest frequency within this hectad rather than absence. To reflect this, frequency scores were expressed on a scale ranging from 1 (least frequent) to 5.

Population abundance

Abundance was measured as the maximum density of individuals within a population, based on samples of randomly placed quadrats in the densest area of the population. For *C. arvense* and *C. heterophyllum*, abundance was recorded as the number of shoots within two 1 × 1 m quadrats at each site; for *C. acaule* abundance was based on the number of clumps rather than individual shoots and recorded from two 5 × 5 m quadrats. Quadrat size was larger for *C. acaule* because this species occurs as scattered individuals rather than the dense stands that are typical of *C. arvense* and *C. heterophyllum*.

Plant communities

Two community surveys were conducted in each population. Per cent shoot frequency of each species present was calculated based on presence in each of 25 cells of a 50 cm × 50 cm strung quadrat (Goldsmith *et al.*, 1986). Quadrats were placed randomly within the densest area of the population.

Morphological traits and seed production

The traits measured in each species are listed in Table 2. Owing to access agreements made with conservation authorities in the Peak District National Park, UK, it was not possible to perform any destructive analysis (e.g. biomass) on *C. acaule* or *C. heterophyllum* in this area. Consequently, with the exception of the collection of seed heads, all measures were nondestructive. Collection of seed heads was restricted to less than 30% of those produced by each population studied.

Within each population, 30 plants were chosen at random and the traits measured as listed in Table 2. *Cirsium acaule* rarely produces a flowering stem, flowering instead within the rosette. Clump diameter was used as an additional measure of plant growth (as opposed to height) in this species. The total number of capitula produced per plant was not recorded for *C. acaule* because of the indeterminate flowering of populations of this species within a season. The ratio leaf length to leaf width was used as an indication of leaf shape, while leaf length indicated leaf size (Mooney & Billings, 1961; Rochow, 1970).

To assess seed production, 30 ripe but not dehiscent capitula were collected at random within each population. In *C.*

Table 2 Morphological and seed traits measured in the *Cirsium* species investigated

Species	Characters measured (n = 30)
All species	Maximum length and width of youngest fully expanded leaf (excluding petiole) Total filled seed mass per capitulum Percentage of population failing to set seed
Cirsium acaule only	Maximum clump diameter
Cirsium arvense and *C. heterophyllum* only	Height at flowering Number of flowers per plant

arvense these were chosen only from female flower heads (Moore, 1975; Heimann & Cussans, 1996), in *C. heterophyllum* the terminal capitulum was selected from the flowering stem of each plant. Capitula were air dried in paper envelopes for 1 month before deseeding. Seeds were extracted from each capitulum by removing the pappus material and seeds and rubbing this across a soil sieve (4 mm mesh). The seeds collected were then cleaned of debris and sorted by hand using a hand-lens to separate entire, filled seed from unfilled seeds and those damaged by insect predation. Damage due to seed predation was scored between 0 and 4 for each capitulum. Total filled seed mass per capitulum was recorded.

Data analysis

Community data were analysed using a combination of classification and ordination methods. Such methods are usually used to identify particular phytosociological groups, however, our aim in the analysis of these data was to identify outlying samples (rather than the main clusters) to determine whether the peripheral populations of *C. acaule* and *C. heterophyllum* occur in atypical communities. A potential problem with this approach is that different methods for the analysis of community data are likely to deal with outlying samples in different ways (Gauch & Whittaker, 1981). The most informative approach is thus to use several different methods of analysis on the same data set and compare the results to get a more comprehensive view of the data structure (Kent & Ballard, 1988).

Community data were classified using the agglomerative increase sum of squares method, followed by calculation of sample proximities based on squared Euclidean distance, using the program CLUSTANGRAPHICS (Wishart, 1999). An additional divisive classification was produced using the default parameters of the programme TWINSPAN (Hill, 1979a; Malloch, 1999). Community ordination (detrended correspondence analysis, DCA) was performed using the default parameters of the programme DECORANA (Hill, 1979b; Malloch, 1999). See Kent & Coker (1992) for a detailed description of these techniques. The authors of these programmes (M. Hill and A. Wishart) were contacted to confirm the validity of this approach.

Population density and abundance, seed production and morphological characters were regressed against latitude using SIGMAPLOT 2001 for Windows v7 (SPSS Inc. Chicago, IL, USA).

Results

Population density

A significant relationship was found between maximum population frequency and latitude in *C. acaule* (Fig. 2a, $R^2 = 0.82$, $P < 0.0001$) and *C. heterophyllum* (Fig. 2b, $R^2 = 0.42$, $P < 0.05$). Both species occur with highest population frequency in core areas of their range and decrease toward the periphery. Owing to the reduced maximum frequency of *C. heterophyllum* in the far north of Scotland, a quadratic relationship better describes the relationship between frequency and latitude than a straight line (linear regression: $R^2 = 0.20$, $P = 0.064$). The widespread *C. arvense* shows no variation of maximum population frequency with latitude (Fig. 2c). Maximum population frequency in this species is at the maximum value of 5 throughout almost the entire length of the UK, only one latitude in the far north of Scotland has a maximum population frequency less than this. At this latitude only a single survey was possible, this was conducted in a predominantly coastal region.

Population abundance

There was a significant relationship between latitude and within-population abundance only in *C. heterophyllum* (Fig. 3, $R^2 = 0.36$, $P < 0.01$). Abundance in *C. heterophyllum* is highest in the core area of its UK distribution in central Scotland and declines approaching its southern range edge. No relationship was found between latitude and abundance in either of the other species.

Community composition

The DECORANA community ordination is presented in Fig. 4. Most of the separation of the community types in the ordination is accounted for by axis 1 (eigenvalue 0.72), with axis 2 (eigenvalue 0.38) and axis three (eigenvalue 0.25) accounting for much less. The communities of geographically

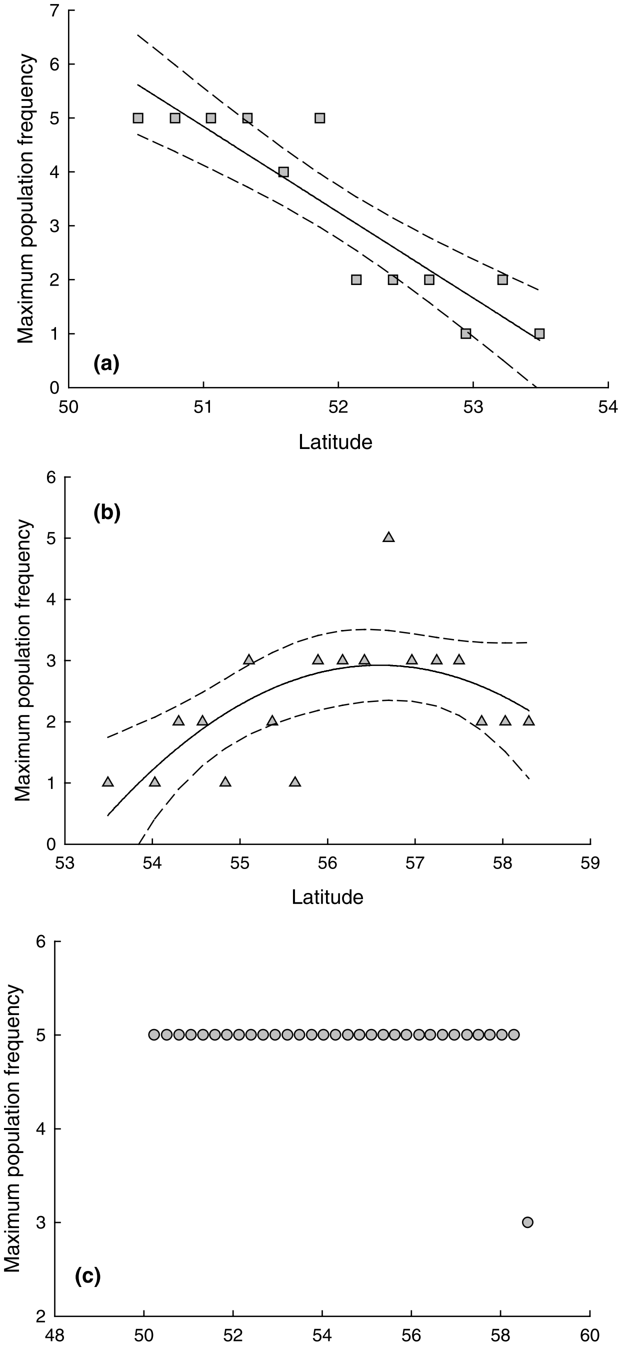

Fig. 2 Maximum population frequency as a function of latitude. (a) *Cirsium acaule* ($y = 68.0 - 1.59x$, $R^2 = 0.82$, $P < 0.0001$). (b) *Cirsium heterophyllum* ($y = -813 + 28.8x - 0.255x^2$, $R^2 = 0.42$, $P < 0.05$). (c) *Cirsium arvense*. Dotted lines show 95% confidence limits of regression.

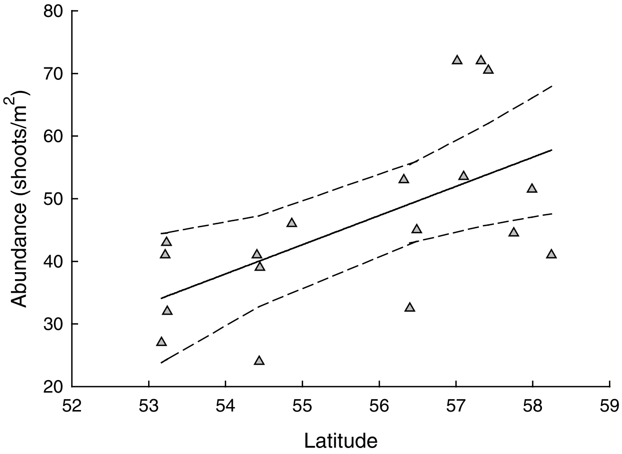

Fig. 3 Mean abundance of *Cirsium heterophyllum* as a function of latitude ($y = -213 + 4.66x$, $R = 0.36$, $P < 0.01$). Dotted lines show 95% confidence limits of regression.

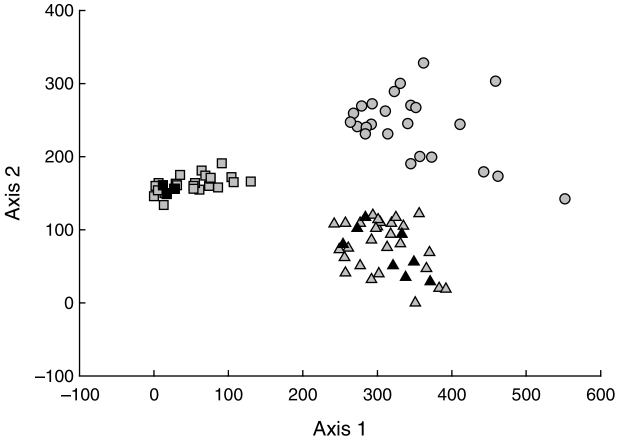

Fig. 4 Community ordination as produced by DECORANA. Squares, communities surveyed for *Cirsium acaule*; triangles, communities surveyed for *Cirsium heterophyllum*; circles, communities surveyed for *Cirsium arvense*. Black symbols represent communities in peripheral regions of the geographical range of *C. acaule* and *C. heterophyllum*.

peripheral populations of *C. acaule* and *C. heterophyllum* occur in the centre of the ordination clusters rather than as outliers. This result is supported by the community classifications, which also classify peripheral populations in the centres of the main community clusters (data not shown). The community ordination and classification analyses used here suggest that peripheral populations of *C. acaule* and *C. heterophyllum* do not occur in atypical communities.

Morphological traits

In *C. acaule* there is a significant relationship between clump diameter and latitude ($R^2 = 0.53$, $P < 0.01$, data not shown). Clump size is smallest (25.5 cm) in the core populations of this species and increases toward the periphery (48.5 cm). There is no relationship between any other vegetative character measured and latitude in any of the species investigated.

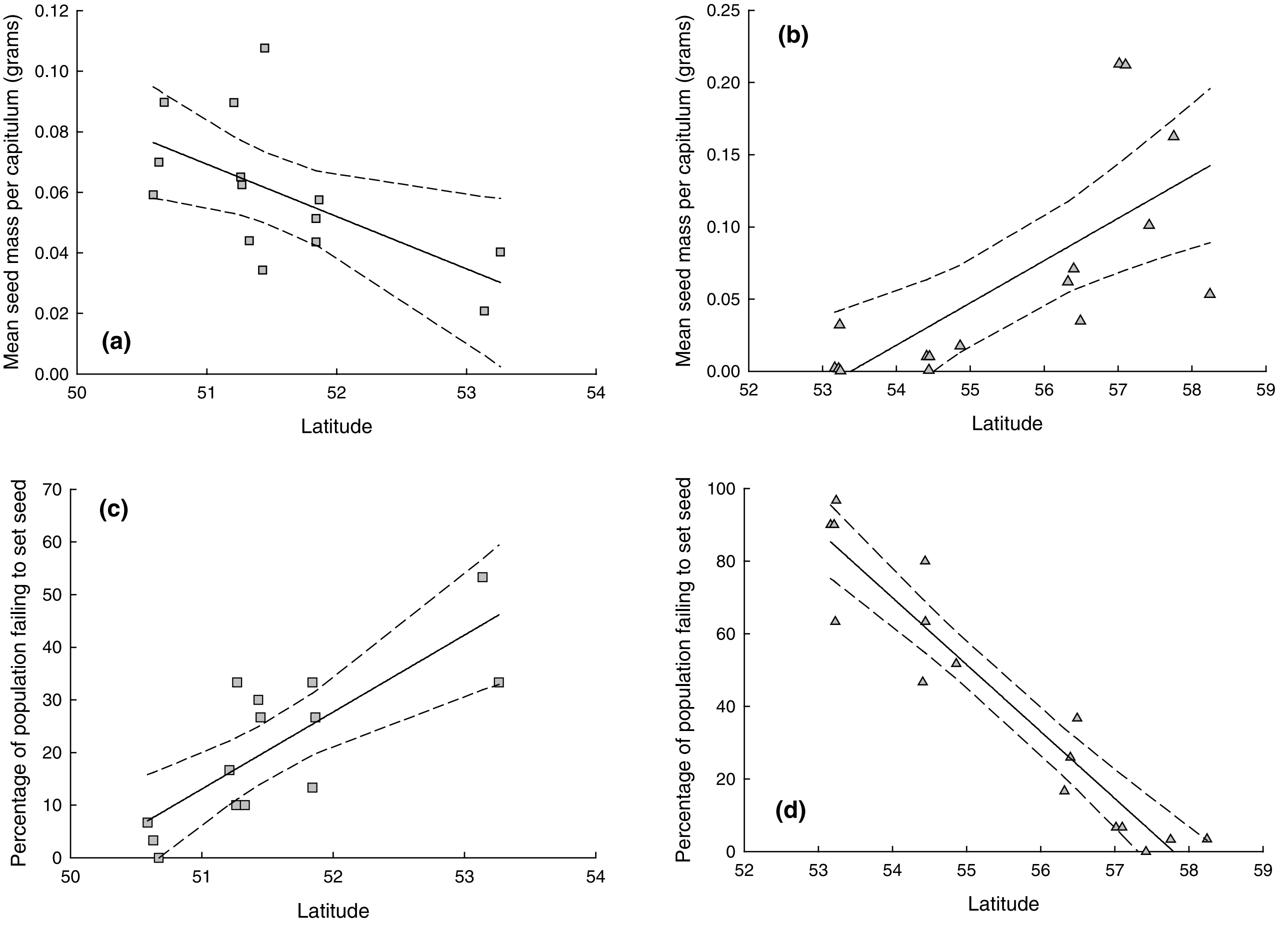

Fig. 5 Seed production in *Cirsium* species as a function of latitude: Mean total filled seed mass per capitulum: (a) *C. acaule* ($y = 0.951 - 0.0173x$, $R^2 = 0.35$, $P < 0.05$); (b) *C. heterophyllum* ($y = -1.56 + 0.0293x$, $R^2 = 0.51$, $P < 0.005$). Percentage of population failing to set seed: (c) *C. acaule* ($y = -733 + 14.6x$, $R^2 = 0.63$, $P < 0.001$); (d) *C. heterophyllum* ($y = 1066 - 18.4x$, $R^2 = 0.90$, $P < 0.0001$). Dotted lines show 95% confidence limits of regression.

Seed production

A significant relationship between seed production and latitude was found in both *C. acaule* (Fig. 5a, $R^2 = 0.35$, $P < 0.05$) and *C. heterophyllum* (Fig. 5b, $R^2 = 0.51$, $P < 0.005$). A preliminary study of seed production in *C. heterophyllum* conducted in 1999 yielded a similar result ($R^2 = 0.73$, $P < 0.01$; data not shown). In both species, seed mass per capitulum declined approaching the periphery. This decline is most dramatic in *C. heterophyllum*, which at its southern periphery produced only 1.2% of the maximum seed mass recorded in the core area of its UK distribution. Maximum seed production in *C. acaule* at its northern periphery was 37% of the maximum recorded in the core area of its distribution in southern England.

In both *C. acaule* and *C. heterophyllum* there is a parallel pattern in the percentage of the population that fails to set any seed. Both show a significant rise in failure to set seed toward their peripheral latitudes (*C. acaule*: Fig. 5c, $R^2 = 0.63$, $P < 0.001$; *C. heterophyllum*: Fig. 5d, $R^2 = 0.90$, $P < 0.0001$). In *C. heterophyllum* the maximum percentage of individuals bearing seed within any peripheral population is 37% compared with 100% in the core area of its distribution. *Cirsium acaule* shows a similar decrease in seed-bearing individuals toward its northern periphery. In the peripheral populations, a maximum of 47% of individuals were found to set seed as opposed to a maximum of 100% in core populations. Subsequent investigation of the viability of any filled seed produced suggested this did not vary with latitude (data not shown).

There is no relationship with latitude in either mean seed mass per capitulum or the percentage of the population failing to set seed in *C. arvense*, neither is there a significant decline in flower production in *C. arvense* or *C. heterophyllum* across their geographical range in the UK. Seed predation did not appear to vary with latitude in these species despite a report by Tofts (1999) that such a pattern occurs in the related species *Cirsium eriophorum*.

Discussion

Hengeveld & Haeck (1982) proposed the general biogeographical rule that species become rarer toward their range margins, independent of the spatial scale of observation. They predicted that declining environmental favourability with increasing distance from the core of a species range would lead not only to a decrease in favourable habitat patches, but also a decline in the favourability of any patches that occur; thereby leading to a decline in both density and abundance (Brown, 1984). Although population density declines approaching the periphery of both *C. acaule* and *C. heterophyllum*, only in *C. heterophyllum* is this accompanied by a decline in abundance within populations; *C. acaule* does not fit the pattern of parallel decline in abundance predicted by both Hengeveld & Haeck (1982) and Brown (1984). Sagarin & Gaines (2002) found that only 39% of the studies that they reviewed supported the predicted decline in abundance. *Cirsium acaule* may favour an alternative pattern discounted by Hengeveld & Haeck (1982), that the number of favourable habitat patches may decline approaching the range boundary but that abundance within them remains the same – a pattern also reported by Pérez-Tris *et al.* (2000). This may, in some part, be explained by the great sensitivity of *C. acaule* to summer irradiance (Pigott, 1968) acting more in terms of a presence/absence (threshold) effect in this species rather than the gradual decline predicted to result from the processes described by Brown (1984).

There is no support from community surveys of *C. acaule* or *C. heterophyllum* for the prediction that peripheral populations will occur in atypical habitat. There is only limited support for this prediction in the literature. For example, Fernald (1925) described a mixing of species typical of northern North America with those typical of southern states of the USA, in rare communities at the edge of their geographical ranges. Barden (2000) described southern peripheral populations of the common shrub *Quercus ilicifolia*, which occur in a rare community type not seen in other areas of the species range. However, since species are often found in a greater variety of habitat types in core rather than peripheral areas of their distribution (Hall *et al.*, 1992; Pérez-Tris *et al.*, 2000) it may be more likely that, at the periphery, they will be restricted to only the most favourable of these, rather than occurring in novel habitat unoccupied elsewhere in the range.

Despite the general absence of latitudinal patterns of morphological traits in these species, there is a significant increase in clump size in *C. acaule* approaching the periphery of this species. This trait is not comparable with plant size traits measured in the other *Cirsium* species, since, in *C. acaule*, clump size refers to the size of individual genets rather than the size of ramets measured as morphological traits for the other species. It may be more accurate to view clump size as an indicator of vegetative reproduction rather than plant size. If so, this raises questions as to whether this may occur as a result of reproductive assurance (Pannell & Barrett, 1998) in this species, given that vegetative offspring may have a greater chance of survival in peripheral populations compared with plants produced by seed (Eckert & Barrett, 1993).

When considered alongside the absence of patterns in morphological traits, the decline in seed production approaching the range edge of *C. acaule* and *C. heterophyllum* suggests that reduced reproductive success rather than vegetative survival may limit the geographical distribution of these species in the UK. This pattern is in agreement with that described for many plant species (Pigott & Huntley, 1981; Reinartz, 1984b; Eckert & Barrett, 1993; García *et al.*, 2000; Dorken & Eckert, 2001). Climate is implicated in determining the distribution of *C. acaule* and *C. heterophyllum* (Pigott, 1968; Conolly & Dahl, 1970), Pigott (1968) noted a reduction in seed production in *C. acaule* at its northern limit linked to the reduced heat sum gained by the capitula of northern populations. Despite this, some viable seed is produced (indicated by the presence of seedlings in both peripheral populations in 2000). Although a decline in seed production approaching the range edge is reported frequently, recruitment by seed is likely in peripheral populations since pronounced interannual variation in both climate and seed production occurs (Pigott, 1968; Pigott & Huntley, 1981; Houle & Filion, 1993; Despland & Houle, 1997; Woodward, 1997). However, production of viable seed does not necessarily result in the expansion of a species' geographical range, since recruitment depends on seed production, seedling establishment and seedling survival (Pigott, 1992; Dorken & Eckert, 2001).

In species that combine seed production with vegetative spread, clonal reproduction allows populations to persist in the absence of recruitment by seed (Ellstrand & Roose, 1987; McLellan *et al.*, 1997; Dorken & Eckert, 2001). Since each of the species investigated here employs both these means of reproduction, the marked reduction in seed production does not imply that populations should be unable to persist at the range edge. However, the founding of new populations of these species will be largely dependent on the dispersal of viable seed and subsequent plant establishment. If the decline in the density of populations reported here is interpreted as indicating a decline in density of favourable habitat patches (Brown, 1984), range expansion may be limited by the combined effects of reduced seed production and decreased probability of successful dispersal to (increasingly distant) favourable sites. Levels of seed production (and hence seed dispersal) at the periphery may be below those required for the successful establishment of new populations (Primack & Miao, 1992) despite the production of some viable seed by existing populations.

Environmental stress levels are expected to rise toward a species periphery as a result of declining environmental favourability (Parsons, 1991; Hall *et al.*, 1992). A predicted consequence of this is a decrease in energy available for growth and reproduction approaching the range edge and hence a decline in plant size and the production of seed. The geographical limit for vegetative survival and that for the production of viable seed may, however, be determined by very different environmental conditions (Woodward, 1997) and sometimes widely separated in space (Woodward, 1990). At geographical limits where species can grow and complete a normal life cycle, successful regeneration is not guaranteed even if viable seed is produced; thus, the realized range of a species in the natural environment may differ from that which it might theoretically occupy based on vegetative survival (Pigott, 1992). The proposed effect of stress might not be seen on plant growth if a species' distribution is limited by poor reproduction. The range limits of *C. acaule* and *C. heterophyllum* may result from reduced seed production acting in combination with a decrease in the availability of favourable habitat patches; the combined effect of these factors may make the establishment of new populations unlikely. These species are therefore likely to be absent from the region that is expected to be highest in stress (due to poor reproduction), despite the fact that they might survive vegetatively in this area. Consequently, since the effects of declining environmental favourability are more likely to be detected through reduced reproduction, the proposed effects of stress may not be detectable as a reduction in growth in the natural environment.

Conclusion

In *C. acaule* and *C. heterophyllum* there is no support for the prediction that peripheral populations will occur in atypical habitat, or that a reduction in plant size will occur approaching the range edge. In both these species, however, there is a marked reduction in seed production approaching the range edge, demonstrating that reduced reproductive output of peripheral populations may be of critical importance in restricting plant geographical ranges. The decline in population density also observed approaching the range edge of these species may interact with reduced reproductive output to reduce the probability that new populations will establish in peripheral areas of the species distribution. Both decreased density and reduced reproduction of peripheral populations may have consequences for the genetic structure of populations of these species at the range edge. This is investigated in a companion paper.

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