Plant Ecology **166:** 167–188, 2003.

Ecological investigations on the northern distribution range of *Hippocrepis comosa* L. in Germany

Klaus Josef Hennenberg[1] and Helge Bruelheide[2,*]
*[1]Institut für Biodiversitätsforschung, Allgemeine und Spezielle Botanik, Universität Rostock, Wismarsche Str. 8, Rostock, D-18051, Germany; [2]Albrecht-von-Haller-Institute for Plant Sciences, Dep. of Ecology and Ecosystem Research, University of Göttingen, Untere Karspüle 2, D-37073 Göttingen, Germany; *Author for correspondence (e-mail: hbruelh@gwdg.de; fax: ++49-551-393556)*

Received 11 February 2000; accepted in revised form 7 November 2001

Key words: Biogeography, Establishment, Frost hardiness, Geographical range, Germination rate, Growth analysis, Microclimate, Phenology, Plant distribution, Regression, Survival

Abstract

The objective of this study was to identify the causes of the limits of the geographical range of *Hippocrepis comosa*. Along a gradient from the northwestern distribution boundary towards the distribution centre in Germany, 46 field plots were established where growth and microclimate were monitored simultaneously. In total, 11 vegetative and generative traits and 7 microclimatic parameters were recorded over 7 time intervals during the vegetation period, together with 14 general site parameters. Regression analyses were performed between all traits and environmental parameters in a certain interval. At the beginning of the growing season the best positive correlation coefficients for vegetative growth were observed with soil temperature. From the end of May to the middle of June, vegetative growth rates decreased and showed the best positive correlation with soil water content. Despite credible relationships between vegetative growth and microclimate, their contribution toward explaining the northern distribution boundary was found to be limited, because no correlation with the distance from the distribution boundary was observed. The only growth parameter that showed both a positive correlation with distance from the distribution boundary and a significant correlation with microclimate was the percentage of seed setting, which increased towards the distribution centre and was correlated with air temperature. Further field observations on plots outside the actual range of *Hippocrepis comosa* revealed no microclimatic reasons as to why the species was absent from these sites. This shows that the environmental parameters are in no way deterministic for the range limit. The frost hardiness of *Hippocrepis comosa* was studied in additional laboratory experiments in which significant damage was not found above −18 °C for adult plants and above −14 °C for seedlings, which is remarkably low and too low to be relevant for the northwestern distribution boundary. Another field experiment revealed that seedling establishment exhibited a positive relationship to soil water content, which became more favourable towards the range boundary. It is concluded that temperature, particularly air temperature, makes the largest contribution to explaining the northern distribution boundary of *Hippocrepis comosa* in Germany and that mainly generative reproduction is affected.

Introduction

Geographic distribution ranges of plant species are the result of many interacting factors. Abiotic conditions at a site have to match the specific requirements for a certain species and the species' dispergules have to arrive and establish themselves at this site (Urbanska 1997; Bonn and Poschlod 1998). Among all abiotic parameters, climate is thought to be of primary importance for limiting geographic distribution ranges (Good 1964; Walter and Straka 1970; Woodward 1987, 1992). By superimposing distribution maps with climatic maps, Jäger (1972, 1990, 1995) was able to point out the relevant factors for the range

limits of a large number of plant species. He found good correlations with winter and summer temperature, temperature sums and the amount of precipitation. For example, some winter annual plants such as *Scandix pecten-veneris* are limited by a mean January temperature of less than −4 °C (Jäger 1990). Huntley et al. (1995) used only three climatic variables to predict species distribution in the 50 km-grid cells of the *Atlas Florae Europaeae* (Jalas and Suominen 1972–1991). For example, *Pulsatilla vulgaris* as a species of xerophilous grasslands is limited to areas with a temperature sum above a 5 °C-threshold of more than 1000 but less than 3000 day degrees, with a mean temperature of the coldest month between −7 °C and −9 °C and with an estimated ratio of actual to potential evapotranspiration above 0.7. Other examples of modeling plant distribution ranges to climatic variables are given by Box et al. (1993); Holten (1993); Saetersdal and Birks (1997). All the climatic variables used in this kind of studies refer to the macroclimate. This is appropriate when attempting to identify correlations on a global scale to continental one but with increasing resolution, i.e. on a regional or local scale, microclimate becomes more and more important. For example, the climatic variation between the north- and south-facing slopes of the same hill may be much greater than the variation between equally exposed sites separated by a distance of 100 km. Consequently, climatic recordings taken at a more or less remote official meteorological station using standard measuring conditions are only of limited value on a regional scale. Instead, microclimatic data are needed that are measured directly at the field site where the plant under consideration is growing (Grace 1987).

The shift from a global to a regional scale presents the opportunity to investigate the operating mechanisms rather than merely the final effects (see Woodward (1997)). Although the final effect is always the presence or absence of a species, the operating mechanisms may act on very different aspects of plant growth, e.g. influencing vegetative growth or reproductive success. The determination of the relevant factors for a certain distribution boundary can be very troublesome and puzzling. For example, Pigott and Huntley (1978, 1980, 1981) demonstrated that the northern distribution limit of *Tilia cordata* in England is due to low temperatures in summer, which do not allow an adequate pollen tube growth rate, thus resulting in failure to fertilize the ovary within the lifespan of the pollen tube. Another intricate mechanism determining plant distribution is the selective herbivory of plants when the herbivore is climatically controlled. An example is the altitudinal distribution of *Arnica montana* caused by increased slug grazing at lower elevations (Bruelheide and Scheidel 1999; Scheidel and Bruelheide 1999). It is quite obvious that the crucial mechanisms will probably differ from species to species. Consequently, on beginning an investigation of a specific distribution boundary a systematic study will be advantageous for screening a large variety of plant response variables for a relationship with climate.

Such a study was performed with *Hippocrepis comosa* L. (horseshoe vetch) at its northern distribution limit in Germany using a large number of field sites where growth and microclimate were recorded simultaneously. The field sites were established along a line from the distribution boundary of *Hippocrepis comosa* towards its distribution centre in Germany. Our first objective was to test whether there is a microclimatic gradient towards the distribution boundary.

The second and main objective was to present correlations between growth and microclimate for various time intervals of the species' growth period. Special emphasis was placed on the reproduction of *Hippocrepis comosa* since Fearn (1973) hypothesized for Britain that "the northern and western limits of the species are (....) probably determined by a scarcity of long, warm, dry summers to induce flowering and to ripen the fruits before the onset of autumn frosts." In addition to testing correlations, sites close to the distribution boundary were compared to central sites with respect to growth and microclimate.

All plots mentioned only included field sites where the species was present. However, this approach is not appropriate for explaining why the species is absent outside its distribution range. For this purpose we included sites close to the distribution limit where the species could be expected to grow but did not actually occur. It was our third objective to test whether the microclimatic conditions of colonized sites were more favourable than those of non-colonized sites.

All the climatic parameters we had monitored in our study were only measured during the spring and summer. For a submeridionally distributed species such as *Hippocrepis*, the microclimate outside the vegetation period, especially the frosts in winter, might be of equal or even greater importance than the microclimate in the growing season. Therefore, our fourth hypothesis was that some life stages of *Hippocrepis* were particularly susceptible to frost damage.

The frost experiments also included seedlings, thus taking the fact into consideration that the most vulnerable time in the life cycle of a plant is the seedling stage (Harper 1977).

In addition to laboratory experiments, we also investigated seedling establishment in the field. The fifth and last objective of this article was to test to what degree seedling establishment is influenced by microclimate.

Materials and methods

Study species

Hippocrepis comosa (Fabaceae) is a long-lived, polycarpic perennial herb with prostrate stems and woody base (Hegi 1924). The woody tap-root extends down to a depth of 90 cm and may be strongly branched (Fearn 1973). Its shoots and a large part of their imparipinnate leaves are retained throughout the winter (Fearn 1973). With regard to the position of overwintering buds, the species is intermediate between a hemicryptophyte and a chamophyte (Ellenberg 1992).

The plant reproduces amost exclusively by means of seeds, although clonal growth may occur by layering of branches and development of adventitious roots (Söyrinki 1954; Fearn 1973). In Germany, the flowering period starts at the end of May and continues until the beginning of July. The flowers are arranged in heads of 4 to 12 with a peduncle of 5–10 cm. The pods have a length of 10–30 mm, are covered with fine papillae and break up into (1) 3–6 (10) horseshoe-shaped segments, which gave the species its common name, horseshoe vetch. The seeds are 2.6–4.2 mm in size and weigh 1.5–4.0 mg. Seeds or fruit segments are dispersed about three months after flowering. In dry seasons the segments break off and release a single seed; in wet seasons the seeds remain in the segments and are not liberated before the pod wall has rotted (Fearn 1973). There is no special dispersal mechanism. Although anemochory was previously assumed (Hegi 1924; Kirchner et al. 1938), the prostrate growth habit of the species with fruits being shed close to the ground renders wind dispersal hardly effective (Greene and Johnson 1989). The species is probably mainly dispersed by sheep (Fischer et al. 1995), although this kind of dispersal has not been observed in all studies (Poschlod et al. 1998). It is highly probable that the most effective dispersal mechanism is the combined transport of seeds and soil material adhering to the hooves of sheep and cattle (Fischer et al. 1996; Stender et al. 1997; Bonn and Poschlod 1998). From the data given by Thompson et al. (1997), it can be concluded that the seeds are short-term persistent, e.g. at minimum one year and at maximum five years surviving in the soil. Controversely, the investigations of Poschlod and Jackel (1993) and Poschlod et al. (1998) indicated a persistence up to 25 years in the seed bank.

The species is characteristic of xerophilous grasslands in Germany, preferentially occurring in limestone grasslands (*Festuco-Brometea*) and on rock cliffs (*Seslerietalia*) (Oberdorfer 1978). The main substrates are calcareous soils but *Hippocrepis* also grows on gypsum or even siliceous substrates as granite (Fearn 1973). Fearn (1973) suggests that the species is edaphically restricted to calcareous soils only towards the edge of its geographical range. Several morphologically indistinguishable cytotypes have been described (Fearn 1972). The tetraploid form ($2n = 28$) is the most common one and probably occurs throughout the range of the species (Fearn 1972).

Hippocrepis comosa is restricted exclusively to Europe, where it has a markedly south-western distribution (Figure 1). Occurrences extend from Spain, Sardinia and Greece northwards to northern Germany and England (Meusel et al. 1964). The species is confined to the oceanic and suboceanic regions of Europe, here the northernmost occurrences are found in Britain. In the Alps, *Hippocrepis* exists at altitudes up to 2800 m a.s.l. (Hegi 1924); in the north, the majority of sites are between 60 and 200 m a.s.l. (Fearn 1973).

In southern Europe, *Hippocrepis* is abundant (Hegi 1924; Kirchner et al. 1938); whereas the species becomes rare towards its northern distribution limit (Meusel and Buder 1955; Fearn 1973). In Lower Saxony, where *Hippocrepis* is found growing at the northeastern edge of its distribution range in Germany (Figure 2), the species is included in the Red Data Book as "vulnerable" (Garve 1993).

Site selection

At this species' northern distribution boundary in Germany, 46 plots with natural occurrences of *Hippocrepis comosa* in calcareous grasslands and on rock cliffs were selected along a transect that was approximately 80 km long (T plots, Figure 2). Only sites that were neither grazed nor mowed were included. The sites were classified into habitat types such as open grass-

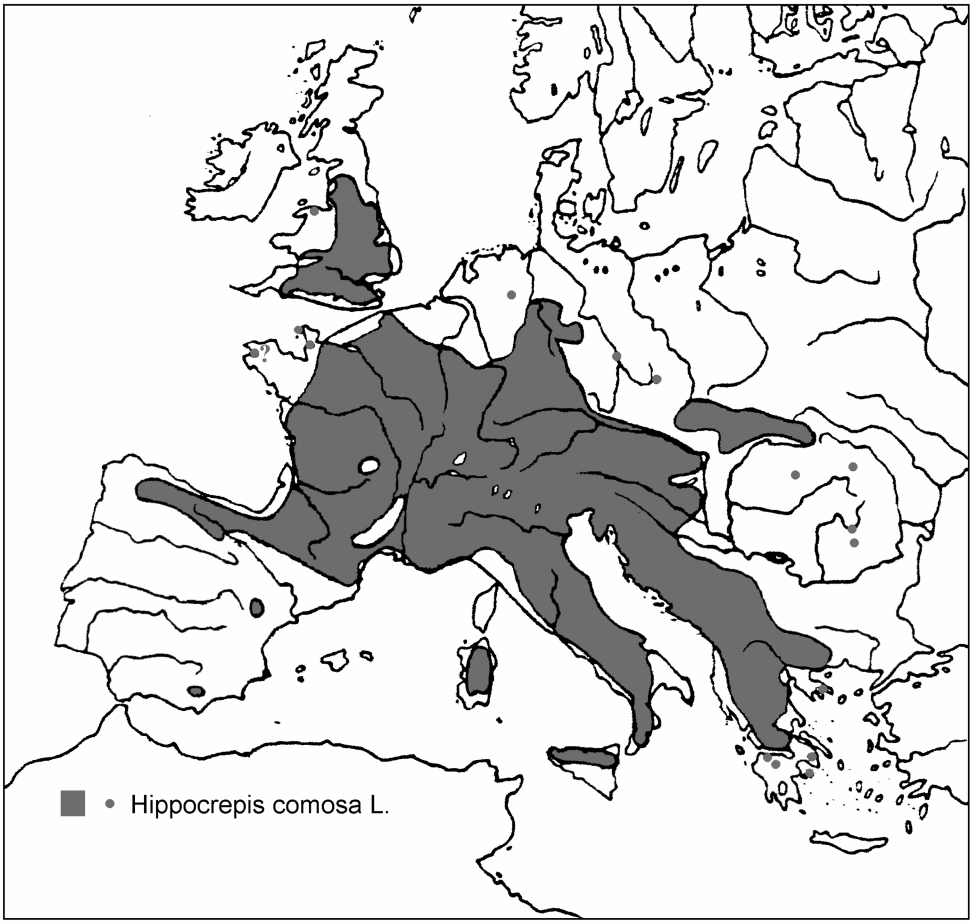

Figure 1. Distribution map of *Hippocrepis comosa* (modified after Meusel et al. (1964)).

land, scrubland, quarry or open pine forest. Since the habitat types were not distributed evenly along the transect, the aim of a fully balanced sampling design was not achieved and at some sites several plots were selected. The sampling within habitats was performed systematically by establishing a circular plot in the centre of each habitat with a diameter of 1 m that was used for monitoring growth and microclimate, and for describing general site conditions.

An additonal 20 plots were placed at the site with the northernmost occurrences directly at the distribution boundary (N plots, Figure 2). Moreover, 18 plots were established in calcareous grasslands outside the distribution range of *Hippocrepis* but in close proximity to the N plots. On these plots (O plots, Figure 2) microclimate and general site conditions were recorded.

Growth parameters

Growth was recorded for generative and vegetative traits on all T and N plots. All parameters and their abbreviations are listed in Table 1. In April 1997 (beginning of interval 1, Table 1), 5 *Hippocrepis* individuals were selected randomly in each plot and marked with a tape ring 2 cm below the shoot's tip. At the end of each time interval shoot length was measured between the tape mark and the tip together with counting internodes and leaves. At the end of the 6th interval (Table 1) the plants were harvested, dried and weighed. The weight was related to the initial weight at the beginning of interval 1, which was based on 5 randomly selected plants at each circular plot described above. For all parameters the absolute growth rate (AGR) and relative growth rate (RGR) were calculated according to Hunt (1989):

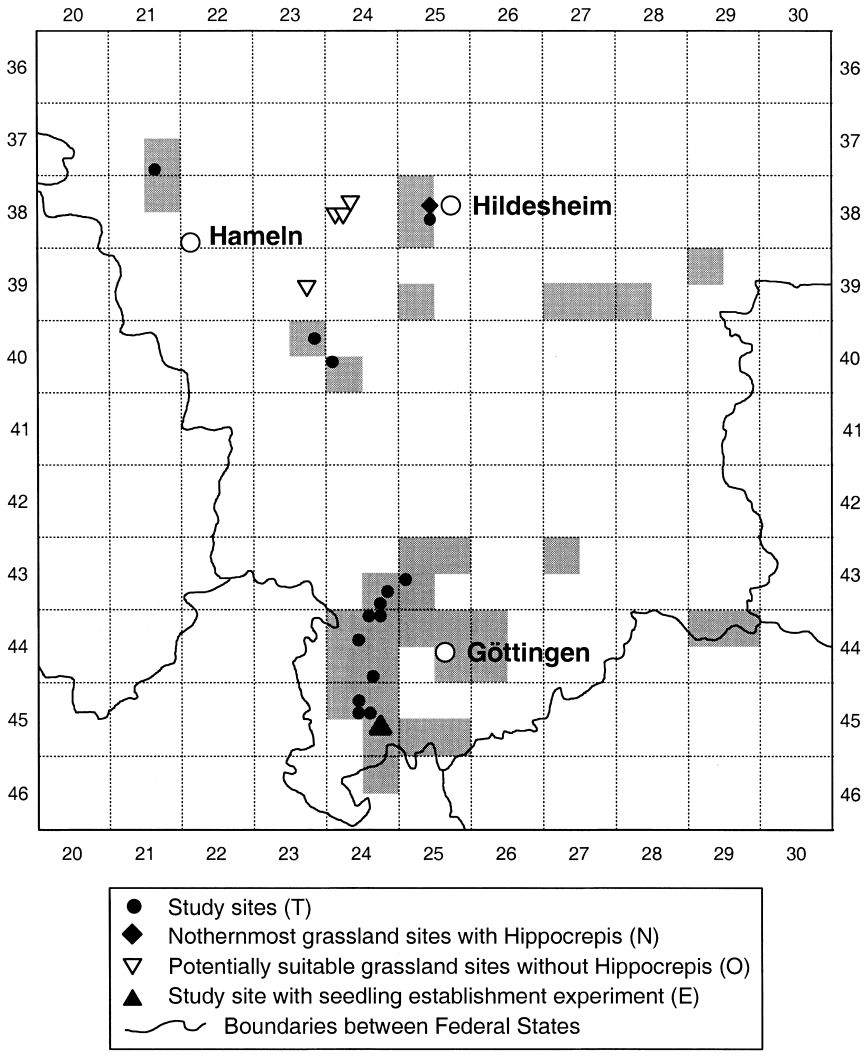

Figure 2. Study area. Symbols indicate sites and may comprise 1 to 6 plots. Numbers refer to the German grid, one cell measuring 6' by 10'. Shaded quarters of squares indicate at least a single occurrence of *Hippocrepis comosa* in Lower Saxony according to data from Garve (1994) and unpublished data from the Lower Saxony Ecology Office (NLÖ).

$$AGR = \frac{x_{n+1} - x_n}{t_{n+1} - t_n} [mm \cdot d^{-1} \quad \text{or} \quad number \cdot d^{-1}] \tag{1}$$

$$RGR = \frac{\ln(x_{n+1}) - \ln(x_n)}{t_{n+1} - t_n} [mm \cdot mm^{-1} \cdot d^{-1} \quad \text{or} \quad number \cdot number^{-1} \cdot d^{-1}] \tag{2}$$

x = shoot length (L), number of internodes (I), number of leaves (N) or dry weight (W)

t = mean date of the interval

AGR and RGR were calculated both for the average of each growth parameter based on all living shoots on the sampling date (M, Table 1) and for the best-growing shoot at a plot (i.e., the longest shoot at the end of the observation interval 3, B, Table 1). Basing the calculations on the best performing plant was thought to reduce possible disturbance effects caused by the experimenter or by biotic agents, e.g. herbivores. In the graphs, RGR was plotted against the mean date of the averaged interval lengths.

For each marked shoot, the number of flowers and the number of pod segments were counted. Since these parameters were extremely variable among the 5 replicates, a larger sample was used by including additional individuals in the plots. In this sample, the

Table 1. Definitions and abbreviations of all measured parameters

Distance from the distribution boundary	
KM	Distance, 0 km is the northermost occurrence of *Hippocrepis comosa*
Growth parameters	
AGR	Absolute growth rate [mm d^{-1}] or [number d^{-1}]
RGR	Relative growth rate [mm mm^{-1} d^{-1}] or [number $number^{-1}$ d^{-1}]
L	Shoot length [mm]
I	Number of internodes
N	Number of leaves
B	Best performing shoot, i.e. the shoot out of 5 replicated plants at a plot with the highest absolute shoot length at the end of observation period 3 (see below).
M	Average of all replicates (5, or less when shoots died) at a plot
1, 2, 3...	Number of observation period: 1 = 2 Apr – 18 Apr to 28 Apr – 4 May 2 = 28 Apr – 4 May to 13 May – 19 May 3 = 13 May – 19 May to 2 Jun – 5 Jun 4 = 2 Jun – 5 Jun to 15 Jun – 19 Jun 5 = 15 Jun – 19 Jun to 11 Jul – 15 Jul 6 = 11 Jul – 15 Jul to 28 Jul – 5 Aug 7 = 28 Jul – 5 Aug to 18 Nov – 21 Nov All growth parameters and environmental parameters refer to these intervals, with the exception of the water content (WC) which always refers to the end of an interval.
1–2, 1–3...	Average over two or more observation periods
thus yielding possible combinations, e.g.:	
	AGR_L_B_1: Absolute growth rate of shoot length of best plant in observation period 1 [mm d^{-1}]
PODNO	Number of pod segments per plant
SEEDSET	Percentage of seed setting in 50 pod segments
SEEDW	Seed weight [mg], refers only to viable seeds
DATEFLOW	Date of peak flowering [Julian day, days counted from 1 Jan = 1]
AGR_W_M	Increase of weight in the total investigation period [mg d^{-1}]
RGR_W_M	RGR of weight averaged over all plants per plot over the total investigation period [mg mg^{-1} d^{-1}]
Structure parameters	
ASPECT	Aspect of site [°] with values between 0 ° and 180 °, N = 0 °, E = 90°, S = 180°, values exceeding 180 ° were substracted from 360 °, thus yielding W = 90 °
SLOPE	Slope of site [°]
HEIGHT_HL	Height of herb layer [cm]
COVER_TL	Cover of tree layer [%]
COVER_SL	Cover of shrub layer [%]
COVER_HL	Cover of herb layer [%]
COVER_ML	Cover of moss layer [%]
COVER_OG	Cover of open ground [%]
COVER_HC	Cover of *Hippocrepis comosa* in the plot [%]
COVER_LI	Cover of litter layer [%]
Soil parameters	
DEPTH_S	Depth of soil [cm]
AW_DEPTH	Available water content calculated on the basis of the actual depth of soil (DEPTH_S) [mm H_2O]
AW_20CM	Available water content calculated on the basis of the actual depth of soil but considering no depths greater than 20 cm [mm H_2O]
PH	pH measured in H_2O
WC	Water content [%] of the soil in the uppermost 2 cm at the end of a certain observation period, e.g. WC_2: Water content of soil at the end of observation period 2; WC_1–4: Water content of soil, averaged over observation periods 1, 2, 3 and 4

Table 1. Definitions and abbreviations of all measured parameters

Microclimate parameters	
All values refer to a certain observation period or an average over several observation periods	
PAR	Potential direct photosynthetic active radiation as portion of the photosynthetic active radiation that measured at an even levelled surface without horizon restriction [%], 100% = 480.5 W m^{-2}, e.g.: PAR_1–3: PAR averaged over observation period 1, 2 and 3 [%]
ET	Effective temperature measured by sugar inversion method [°C]
ET_S	Effective temperature of soil (refering to a soil depth of 7 – 39 mm) [°C]
ET_A_D	Effective air temperature measured at a height of 10 cm above ground (D = down) [°C]
ET_A_T	Effective air temperature measured at a height of 80 cm above ground (T = top) [°C]
RAD_D	Radiation striking a plot measured at a height of 10 cm above ground (D = down), measured by differential measurements of ET
RAD_T	Radiation striking a plot measured at a height of 80 cm above ground (T = top), measured by differential measurements of ET

percentage of set seeds per 50 pod segments and the mean weight of 50 viable seeds were determined.

The date of peak flowering was calculated by estimating the portion of floral buds (B), open flowers (F) and faded flowers (D) in per cent. An index of flowering (IF) was defined as:

$$IF = D - B \tag{3}$$

IF ranges between −100 (= 100% buds) and +100 (= 100% faded flowers). Peak flowering was defined to be when IF = 0, i.e. when number of floral buds and faded flowers were equal (see Sauer (1976); Diekmann (1996)). The date of peak flowering was calculated by logistic regression (MicroCal Origin 3.0):

$$IF = \frac{\min - \max}{1 + e^{\frac{t-b}{c}}} + \max \tag{4}$$

min = lower threshold (set to−100)
max = upper threshold (set to +100)
t = time [Julian day]
b,c = constants

Figure 3 gives examples for the course of IF for two plots differing in 23 days of peak flowering.

Microclimatic parameters

All microclimatic variables were measured at the plot's centre. Effective temperatures for plant growth were determined by the sugar inversion method according to Steubing and Fangmeier (1992):

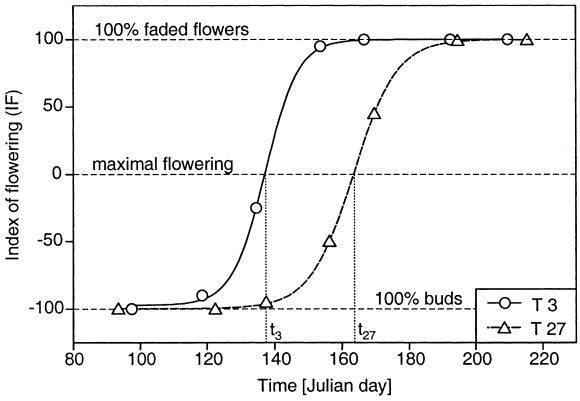

Figure 3. Calculation of peak flowering by logistic regression. t_3 and t_{27} refer to the sites with examples of early and late peak flowering. Peak flowering is the time when the Index of Flowering (IF) is 0 (for details see Methods).

$$eT = \frac{-5856.6}{pH - 20.1998 - \log t + \log[\log(\alpha_A - \alpha_E) - \log(\alpha_t - \alpha_E)]} - 273.15 \tag{5}$$

eT = Effective temperature [°C]
t = Time of exposure [d]
α_A = Initial angle of rotation before exposure
α_t = Angle of rotation after exposure
α_E = Final angle of rotation after complete hydrolysis

The pH of the saccharose solution was adjusted to pH 2.0 in the spring intervals and to pH 2.3 in the summer ones. The method makes use of the exponentially increasing rate of a chemical reaction, thus weighting high temperatures more than low temperatures. Since this chemical method is closely related to

the effect that temperature has on plant growth (Barkman 1977), the result is called the "effective temperature".

To record the effective soil temperature, 20-ml polyethylene flasks containing saccharose solution were buried in the soil at a depth between 0.7 and 3.9 cm.

The effective air temperature was measured by placing the 20-ml flasks behind an insulating shield at heights of 10 cm and 80 cm above the ground. At the same heights two additional black flasks were fixed without an insulation shield. The difference in effective temperature between the unshielded black flasks and the shielded transparent flasks was used as a measure of direct solar radiation (Jones 1983). The effective air temperature and radiation were only measured at 19 plots.

Potential direct photosynthetically active radiation (PAR) was determined according to Wagner (1995). At each plot a skyline profile was taken, with all obstacles that restricted the horizon being mapped. The sun's course over this skyline was calculated for the midpoint of each interval. The time span in which the plants were directly exposed to the sun was taken from the skyline map. For this time span the potential direct PAR was calculated by including aspect and slope and using a temporal resolution of 10 min.:

$$pot.dir.PAR = \left[(3.2\varphi + 0.586\varphi^2 - 0.01103\varphi^3 + 8.68\cdot10^{-5}\varphi^4 - 2.86\cdot10^{-7}\varphi^5) \cdot 0.94\frac{\cos(2\pi\alpha)}{360} + \frac{\sin(2\pi\alpha)\cdot\cos[2\pi(\beta-\gamma)]}{360} \right] / \frac{\sin(2\pi\varphi)}{\cos(2\pi\varphi)} \quad (6)$$

γ = Azimuth
φ = Angle of the sun's altitude
α = Slope
β = Aspect

The soil moisture content was measured gravimetrically. In order to exclude the effect of varying soil texture among the various plots, a standard soil (taken from a rendzina topsoil on Muschelkalk) was used. The soil (ca. 10 g) was filled in bags made of nylon fabric and buried in the uppermost soil layer. When establishing the plots each plot received 10 bags from which one bag each was subsequently sampled at the end of each interval. In contrast to the other microclimatic parameters, the soil moisture content does not refer to a time interval but to a distinct point in time at the end of each interval. Since gathering of bags along the whole transect took approximately four days we tried to exclude systematic sampling errors by randomly varying the sampling sequence of sites.

Those microclimatic parameters that referred to the same interval were used to calculate the regression with growth parameters for this specific interval. In addition, the mean of this parameter averaged over all the intervals from the first one to the interval in question were included in the analyses, thus testing for lag effects.

General site parameters

As general descriptors of plot location, each plot's aspect and slope were recorded (Table 1). The pH (H_2O) was determined for topsoil. Depth of soil was measured by driving a steel rod with a diameter of 1 cm into the soil using 5 replicates. The available water capacity of the top soil was determined by the pressure plate method according to Tan (1996) and used for calculating the amount of available water.

Frost hardiness

The frost tolerance was determined on 3 March 1998 for different organs of adult plants taken from a field site and for seedlings which had developed the first two leaves besides the two cotyledons and had been prehardened before the experiment in a growth chamber at −1 °C. All plants were put with their pots in a freeze chamber and subsequently exposed for 2 hrs. to each of the following temperatures: +4 °C, −10 °C, −14 °C, −18 °C, −22 °C, −26 °C, −30 °C. The cooling rate between levels was 6 °C/h. At the end of each temperature level, a batch of 10 adults and 5 seedlings was removed from the freeze chamber and brought into a growth chamber at +4 °C. In addition, another batch was completely destroyed by putting the plants in liquid N_2. On the next day, leaves, shoots and roots of adults and whole seedlings were put in test tubes with 3% propanol at 4 °C. Frost damage was assessed by measuring conductivity (LF2000, WTW) after t = 0, 3, 7, 13, 26, 55, 93 hrs. The relative conductivity was fitted to a logistic regression (Murray et al. 1989; SAS Institute 1987):

$$RC = \frac{C_i - C_0}{C_A - C_0} = 1 - e^{-k\cdot t} \quad (7)$$

RC = Relative conductivity

C_i = Conductivity after i hrs.
C_o = Initial conductivity
C_A = Conductivity after autoclavation for 10 min.
t = Time in hours after start of measurement

The value of k is a measure of how rapidly electrolytes are released from damaged cells and, therefore, reflects frost injury (Murray et al. 1989). For comparison of frost damage between different plant organs a logistic curve was fitted to k using equation (4) where min = 0, max = 100 and t = temperature. A relative damage of 0% corresponds to k of the 4 °C control and a relative damage of 100% corresponds to the k of the treatment with liquid nitrogen.

Seedling establishment

Field experiments on germination and establishment were conducted on 5 additional plots (Figure 2), which were located in close proximity and varied in vegetation structure: mowed calcareous grassland (E1), open fallow grassland (E2), fallow grassland with bushes (E3), a yellow oat-grass meadow (E4) and bare soil of a stony lithosol (E5). Plots E1, E2 and E3 had natural *Hippocrepis* populations. On each plot 10 subplots of 0.04 m^2 were established; each of them was divided in two halves: one half receiving 50 seeds sown as pod segments and the other one serving as a control for potentially germinating seeds from the natural seed bank. The seeds had been gathered in the surroundings of plots E2 and E3 and then stored for 2 weeks at room temperature before sowing. The pod segments contained 40% viable seeds (triphenyltetrazolium chloride test after Steponkus and Lanphear (1967)). Consequently, each plot received 200 viable seeds on a total area of 0.2 m^2. Based on the 200 viable seeds, a germination rate was calculated as the difference between the number of seedlings observed in the half which received the seeds and the control. Emerging seedlings were recorded regularly and marked for monitoring their survival.

Statistical analysis

Statistics were performed using SAS 6.12. For all regressions, Spearman's rank correlation coefficient was calculated (SAS Institute 1987). Tests of sum of ranks were performed according to Kruskal-Wallis (SAS Institute 1987).

Table 2. Correlations between distance from the distribution boundary and microclimatic parameters. Only the absolute best significant regressions are included ($\alpha < 0.05$), exceeding r = +/- 0.4. For abbreviations see Table 1.

Regressor	Correlation coeff.	Probability	n
ET_A_T_1	0.64789	0.0027	19
RAD_D_4	0.5493	0.0149	19
WC_1	– 0.49117	0.0017	38
RAD_D_5	0.47976	0.0376	19
RAD_T_4	0.46391	0.0454	19
ET_S_2	0.41194	0.0061	43
WC_3	– 0.40783	0.0122	37
WC_4	– 0.40209	0.0151	36

Results

All environmental parameters that show high positive or negative significant correlations of $|r| > 0.4$ with increasing distance from the distribution boundary are listed in Table 2. Towards the distribution centre there is an significant increase in effective air temperature measured in interval 1 at a height of 80 cm above ground (ET_A_T_1), effective soil temperature in interval 2 (ET_S_2) and radiation in interval 4 and 5. In contrast, the water content of soil (WC) decreases with distance in interval 1, 3 and 4. Seed setting was the only growth parameter correlated positively with distance (r = +0.39).

Figure 4 describes the seasonal growth pattern of *Hippocrepis comosa*. The RGR of shoot length as well as that of the number of internodes and leaves reached their maximum in the first weeks of May (interval 2). The AGR was also at maximum at this time, attaining a median of 1.58 mm d^{-1} of shoot length and an absolute length of 260 mm. Variation between plots was considerable, maximum RGR and AGR of shoot length were 0.088 mm mm^{-1} d^{-1} and 10.43 mm d^{-1}, respectively.

Four weeks later (interval 4), the RGRs decreased to 0 (length) or even became negative (internodes and leaves). When the RGRs of vegetative parameters began to decrease, the plants started to produce flowers (Figure 4). Peak flowering was attained between the middle of May and the beginning of June and coincided with the end of vegetative growth. Ripe fruits were found in late July.

Although not directly referring to the T plots, Figure 5 shows the general course of microclimatic parameters in this period. The effective soil temperature increased until the beginning of June and stayed at

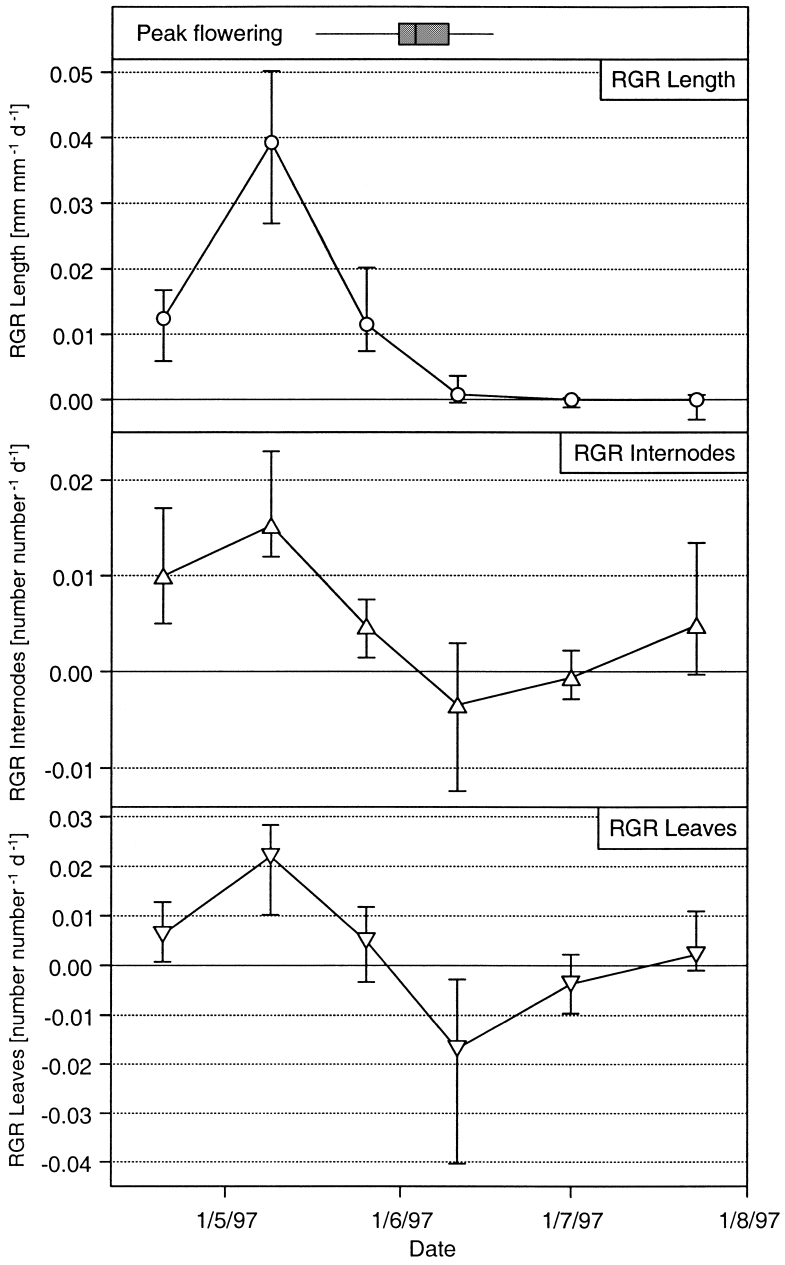

Figure 4. Relative growth rate of shoot length (RGR Length), number of internodes (RGR Internodes) and number of leaves (RGR Leaves), based on the average of all replicates of a plot. Values are medians, error bars are upper and lower quartiles (n = 46 for each date). The box plot for peak flowering gives median, quartiles and extremes for the date when the number of buds equals the number of deflorate flowers and the number of flowers is at maximum (for details see Methods).

around 25 °C until August. Potential direct PAR also increased in spring, attained a maximum in June and decreased thereafter. In contrast, the soil water content displays remarkable fluctuations.

Table 3 summarizes the correlation analyses for all measured environmental parameters by listing only those values that attained the absolute highest correlation coefficients. Some of the highest correlations are illustrated in Figure 6a–6h. All values in Table 3 refer to the Spearman rank correlation coefficient; the figures for the Pearson product moment correlation included in Figure 6 but not shown in Table 3 are very similar.

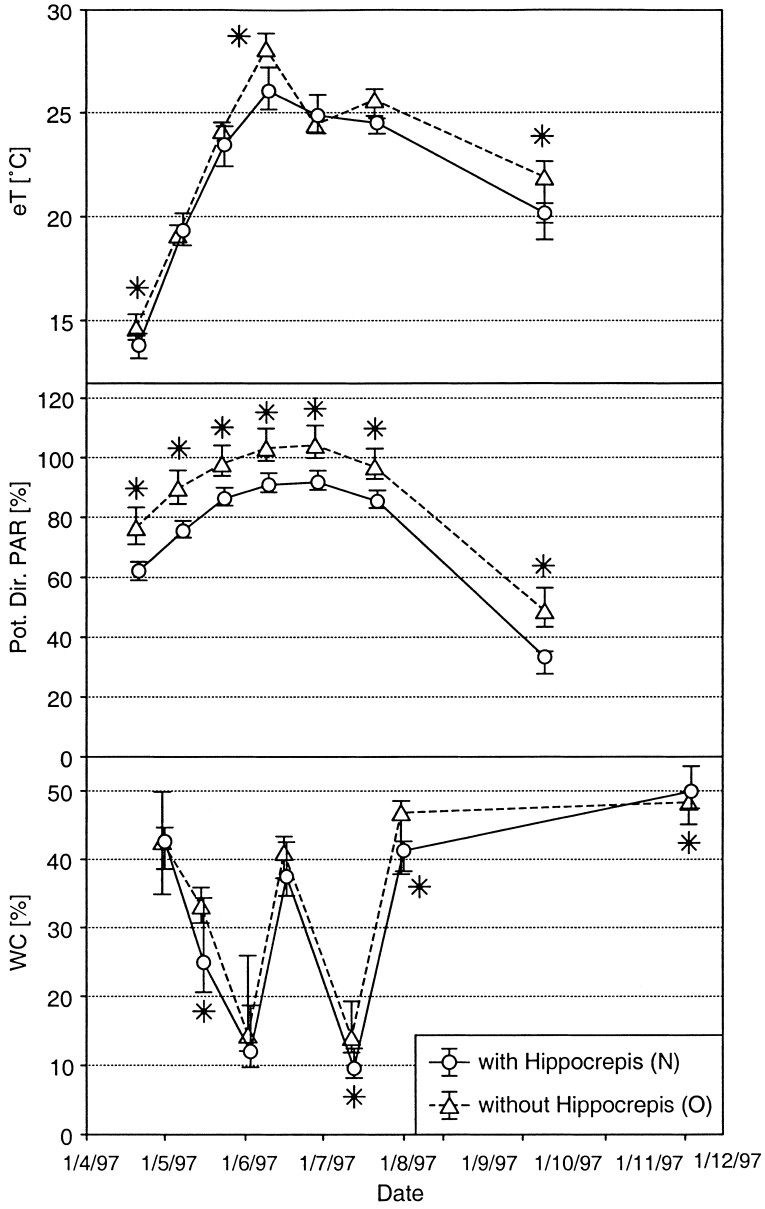

Figure 5. Effective soil temperature (eT), potential direct photosynthetic active radiation (Pot. Dir. PAR) as percentage of pot. dir. PAR of a flat surface without horizon restriction and gravimetric water content of the soil (WC). The graphs for sites with *Hippocrepis* refer to the northernmost occurrences (N plots, n = 17–20 for each date). Sites without *Hippocrepis* are potentially suitable sites near to the sites with *Hippocrepis* but not actually colonized by the species (O plots, n = 11–18 for each date). Values are medians, error bars are upper and lower quartiles. * indicates significant differences on a certain date according to the Kruskal-Wallis test.

The general level of correlation is quite low with only a few correlation coefficients exceeding +/– 0.5. Significant correlations were found for all growth parameters (shoot length, number of internodes, number of leaves) in the first four observation periods. In general, the growth parameters were more positively than negatively correlated with environmental variables in the first two observation intervals and more negatively correlated in the fourth interval. Very often, RGR and AGR were related to the same parameters and showed similar correlation coefficients.

At the start of the investigation (observation period 1, April) growth correlated best with effective soil temperature (ET_S_1). The highest correlation with this environmental variable was encountered for the RGR of internodes based on the average number of

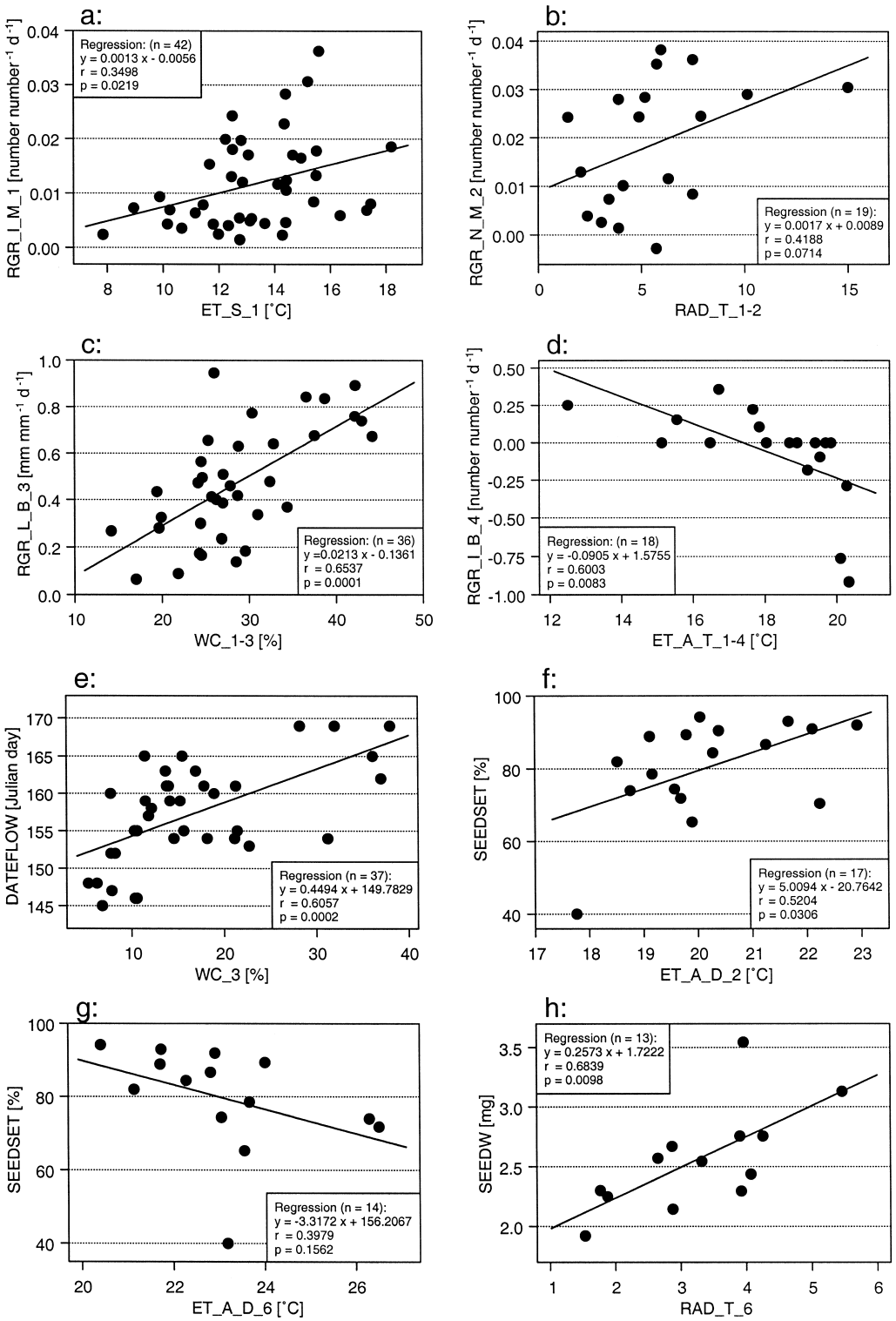

Figure 6. Best regressions of Table 3; a–d refer to vegetative growth in observation period 1–4, e-h refer to generative traits. For abbreviations see Table 1.

Table 3. Spearman rank correlation coefficients of growth with microclimatic and structure parameters. For abbreviations see Table 1. Significant differences ($\alpha < 0.05$) are marked in bold letters.

Parameter	Best positive regressor	Correlation coeffcient	Probability	n	Best negative regressor	Correlation coefficient	Probability	n
RGR_L_M_1	**ET_S_1**	**0.39097**	0.0105	42	ET_A_T_1	–0.44035	0.0592	19
RGR_I_M_1	**ET_S_1**	**0.4815**	0.0012	42	ET_A_T_1	–0.38421	0.1044	19
RGR_N_M_1	COVER_HC	0.2792	0.0664	44	ET_A_D_1	–0.18679	0.458	18
AGR_L_M_1	**ET_S_1**	**0.40297**	0.0081	42	ET_A_T_1	–0.32982	0.1679	19
AGR_I_M_1	**ET_S_1**	**0.43874**	0.0037	42	COVER_TL	–0.23333	0.1229	45
AGR_N_M_1	**WC_1**	**0.34339**	0.0348	38	ET_A_T_1	–0.3405	0.1537	19
RGR_L_B_1	COVER_HC	0.28009	0.0624	45	**ET_A_T_1**	**–0.53169**	0.0191	19
RGR_I_B_1	RAD_T_1	0.32606	0.1867	18	**ET_A_T_1**	**–0.47606**	0.0458	18
RGR_N_B_1	RAD_T_1	0.23113	0.3561	18	ET_A_T_1	–0.44613	0.0635	18
AGR_L_B_1	**ET_S_1**	**0.39799**	0.009	42	ET_A_T_1	–0.33348	0.1629	19
AGR_I_B_1	**ET_S_1**	**0.45571**	0.0024	42	WC_1	–0.31762	0.052	38
AGR_N_B_1	RAD_T_1	0.44549	0.0559	19	ET_A_T_1	–0.42479	0.0698	19
RGR_L_M_2	**WC_1-2**	**0.48597**	0.0027	36	**ET_S_1-2**	**–0.3363**	0.0275	43
RGR_I_M_2	**COVER_ML**	**0.34254**	0.0213	45	**PH**	**–0.3465**	0.0183	46
RGR_N_M_2	**RAD_T_1-2**	**0.53509**	0.0182	19	ET_A_T_2	–0.35789	0.1325	19
AGR_L_M_2	**WC_1-2**	**0.3686**	0.027	36	RAD_T_2	–0.31889	0.1971	18
AGR_I_M_2	**COVER_ML**	**0.33384**	0.025	45	ET_A_D2	–0.24835	0.3053	19
AGR_N_M_2	RAD_T_1-2	0.40351	0.0867	19	ET_A_T_1-2	–0.16491	0.4999	19
RGR_L_B_2	ET_A_T_2	0.36842	0.1206	19	RAD_T_1-2	–0.36491	0.1245	19
RGR_I_B_2	**COVER_HC**	**0.36679**	0.0132	45	ET_S_1–2	–0.24671	0.1107	43
RGR_N_B_2	**COVER_HC**	**0.30836**	0.0393	45	COVER_TL	–0.26099	0.0833	45
AGR_L_B_2	ET_A_T_2	0.43265	0.0643	19	RAD_T_1-2	–0.20877	0.391	19
AGR_I_B_2	ET_A_T_1-2	0.4219	0.072	19	WC_1-2	–0.24037	0.1579	36
AGR_N_B_2	**COVER_HL**	**0.34664**	0.0197	45	PH	–0.2677	0.0721	46
RGR_L_M_3	**WC_1-3**	**0.54801**	0.0005	35	**PAR_1-3**	**–0.61142**	0.0001	44
RGR_I_M_3	**WC_3**	**0.33713**	0.0413	37	**ET_A_D_3**	**–0.48322**	0.0422	18
RGR_N_M_3	**WC_1-3**	**0.4157**	0.0117	36	**RAD_T_3**	**–0.75439**	0.0003	18
AGR_L_M_3	**WC_1-3**	**0.54646**	0.0006	36	**ET_S_3**	**–0.56132**	0.0001	42
AGR_I_M_3	RAD_D_3	0.17033	0.578	13	ET_A_D_3	–0.41507	0.0867	18
AGR_N_M_3	WC_1-3	0.29622	0.0794	36	**RAD_T_3**	**–0.71864**	0.0008	18
RGR_L_B_3	**WC_1-3**	**0.61596**	0.0001	36	**PAR_1-3**	**–0.5845**	0.0001	44
RGR_I_B_3	**WC_3**	**0.34092**	0.0389	37	**SLOPE**	**–0.33009**	0.0251	46
RGR_N_B_3	**COVER_SL**	**0.4112**	0.005	45	COVER_OG	–0.28256	0.06	45
AGR_L_B_3	**WC_3**	**0.58559**	0.0001	37	**PAR_1-3**	**–0.57773**	0.0001	44
AGR_I_B_3	RAD_D_1-3	0.27717	0.2506	19	SLOPE	–0.28929	0.0512	46
AGR_N_B_3	RAD_D_3	0.46911	0.1058	13	ET_A_T_1-3	–0.31732	0.1856	19
RGR_L_M_4	**WC_1-4**	**0.36396**	0.0291	36	**ET_A_T_4**	**–0.51579**	0.0238	19
RGR_I_M_4	**WC_1-4**	**0.40412**	0.0145	36	**ET_A_T_1-4**	**–0.72632**	0.0004	19
RGR_N_M_4	COVER_TL	0.21311	0.1599	45	**ET_A_D_1-4**	**–0.46599**	0.0443	19
AGR_L_M_4	**COVER_TL**	**0.43447**	0.0029	45	**ET_A_T_4**	**–0.56316**	0.0121	19
AGR_I_M_4	RAD_T_1-4	0.34489	0.1482	19	**ET_A_T_1-4**	**–0.57657**	0.0098	19
AGR_N_M_4	WC_4	0.29572	0.0799	36	**ET_A_D_4**	**–0.51273**	0.0248	19
RGR_L_B_4	**COVER_ML**	**0.37467**	0.0122	44	**COVER_LI**	**–0.45205**	0.0021	44
RGR_I_B_4	**WC_1-4**	**0.42773**	0.0104	35	**ET_A_T_1-4**	**–0.78938**	0.0001	18
RGR_N_B_4	WC_1-4	0.29432	0.0911	34	**ET_A_D_1-4**	**–0.72884**	0.0006	18
AGR_L_B_4	WC_4	0.31043	0.0695	35	ET_A_D_1-4	–0.38052	0.1193	18
AGR_I_B_4	**WC_5**	**0.44153**	0.0079	35	**ET_A_T_1-4**	**–0.69789**	0.0013	18
AGR_N_B_4	WC_1-4	0.27984	0.1035	35	**ET_A_D_1-4**	**–0.77511**	0.0002	18
PODNO	RAD_D_4	0.36276	0.1269	19	ET_A_T_4	–0.27492	0.2546	17
SEEDSET	**ET_A_D_2**	**0.5**	0.041	17	**ET_A_D_6**	**–0.60879**	0.0209	14
SEEDW	**RAD_T_6**	**0.65475**	0.0152	13	ET_A_T_2	–0.38872	0.1231	17
DATEFLOW	**WC_3**	**0.57902**	0.0002	37	**PAR_1-2**	**–0.68554**	0.0001	43
AGR_W_M	RAD_T_6	0.45055	0.1059	14	**ET_A_T_1-5**	**–0.54643**	0.0351	15
RGR_W_M	RAD_T_6	0.41099	0.1443	14	ET_A_D_6	–0.38214	0.1598	15

the 5 replicates at a plot (Figure 6a). Another factor related to growth in the first interval was water content of the soil (WC_1). In this interval, most correlations were slightly higher when the growth calculation was based on the average of the five plants per plot than on the best growing plant.

At the beginning of May (observation period 2) the parameters describing the vegetation structure correlated better than microclimatic parameters. For example, the best positive correlation of RGR of internodes was found with the cover of *Hippocrepis comosa* (COVER_HC) and with the cover of the moss layer (COVER_ML, Table 3). RGR of leaf number correlated positively with the cover of the herb layer (COVER_HL). RGR of shoot length was negatively correllated with effective soil temperature averaged over the first two intervals (ET_S_1–2) and RGR of internodes with pH (PH). However, the best correlation was still encountered for a microclimatic variable, i.e. the radiation measured above the herb layer averaged over the first two measuring intervals (RAD_T_1–2), which correlated best with the RGR of number of leaves based on the average at a plot (RGR_N_M_2, Figure 6b). Another microclimatic parameter, water content of the soil averaged over interval 1 and 2 (WC_1–2), correlated best with RGR and AGR of shoot length.

At the end of May (observation period 3) when the RGR began to decrease (compare Figure 4), most growth parameters showed the best positive correlations with the water content of the soil (WC_3, WC_1–3). The highest correlation with r = 0.62 was found for the RGR of shoot length of the best growing plant (RGR_L_B_3, Figure 6c). As in the following observation period, the correlations were slightly better when based on the respective plot's best-growing plant than when based on the average response of the five plants sampled on a plot. In contrast, negative correlations were observed between growth and potential direct PAR (PAR_1_3), radiation measured 80 cm above ground (RAD_T_3), effective air and soil temperature (ET_A_D_3, ET_S_3) and slope (SLOPE, Table 3).

At the beginning of June (observation period 4), the growth rates of length decreased to zero and the growth rates of number of internodes and leaves even became negative (Figure 4). From then on the growth parameters were normally correlated negatively with effective air temperature. Figure 6d gives an example for the RGR of number of internodes of the best growing plant (RGR_I_B4), which was closely negatively related with the effective air temperature measured at a height of 80 cm and averaged over the first four intervals (ET_A_T_1–4). A positive correlation in interval 4 was found for the water content of the soil (WC_4, WC_1–4) and for the cover of the tree and moss layer (COVER_TL, COVER_ML, Table 3).

Table 3 also shows the growth parameters that refer to the whole growing season. To obtain these parameters all recorded environmental variables of all seven observation periods were included in the calculations as well as their averages over the whole growing season. The generative traits also clearly responded to microclimate in a manner similar to the vegetative growth. The best positive correlation of date of peak flowering (DATEFLOW) was found with the water content of the soil at the beginning of June (WC_3, Figure 6e), i.e. the sampling date directly before flowering. This means that the greater the moisture content of the soil, the more retarded was the onset of flowering. In contrast, the date of flowering correlated negatively with potential direct PAR averaged over the first two intervals (PAR_1–2). The number of pods (PODNO) showed no significant correlation. The percentage of set seeds (SEEDSET) exhibited the best positive correlation with the effective air temperature measured 10 cm above the ground at the beginning of May (ET_A_D_2, Figure 6f) and showed the best negative correlation with the same parameter at the end of July (ET_A_D_6, Figure 6g). Seed weight (SEEDW), which refers only to the viable seeds, was well correlated with radiation in July (RAD_T_6, Figure 6h), which is the time when seeds become mature.

The comparison of the northernmost sites with *Hippocrepis* occurrences (N) with all sites along the transect (T) provides no indications of less favourable conditions at the limit of the distribution range in Germany (Table 4). Although the values for ASPECT were lower at the N sites due to mainly western slopes, the effective temperatures of air and soil were no more unfavourable than at the T sites. Water content was significantly higher at the N sites than at the T sites in interval 5 but lower in interval 6. Available water content (AW_20CM) was even higher at the N sites. Similarly, the parameters for vegetative and generative growth differed only rarely between N and T sites. In the first two intervals growth was even better at the N sites. When the N sites did exhibit lower growth rates in the third and fourth interval, the differences were often biologically meaningless. No differences were detected for the generative traits.

Table 4. Comparison of growth and site parameters between the northernmost sites with occurrences of *Hippocrepis comosa* (N) and the sites sampled along the transect (T). Only significant comparisons are included ($\alpha < 0.05$, according to the Kruskal-Wallis test).

Parameter	Site	n	Median	Probability
Site parameters				
WC_4	N	19	37.455	0.0001
	T	34	18.303	
WC_5	N	19	9.553	0.0084
	T	35	17.999	
ET_S_6	N	17	24.509	0.0207
	T	38	23.595	
AW_20CM	N	18	4584	0.0084
	T	44	3868	
ASPECT	N	20	75	0.0009
	T	44	116	
Growth parameters				
AGR_I_B_1	N	20	0.10768	0.0094
	T	44	0.05556	
RGR_N_M_1	N	20	0.01183	0.0446
	T	43	0.00578	
AGR_I_M_1	N	20	0.09908	0.0028
	T	44	0.04781	
AGR_N_M_1	N	20	0.04000	0.0326
	T	44	0.01387	
RGR_L_M_2	N	20	0.05354	0.0047
	T	44	0.03615	
RGR_I_M_3	N	20	0.00064	0.0287
	T	44	0.00433	
AGR_I_M_3	N	20	0.01565	0.0298
	T	44	0.04405	
RGR_L_B_4	N	19	0.00000	0.0239
	T	43	0.01036	
AGR_L_B_4	N	19	0.00000	0.0179
	T	43	0.07229	
RGR_L_M_4	N	20	0.00000	0.0298
	T	44	0.00076	
RGR_N_M_4	N	20	–0.00694	0.0182
	T	44	–0.01919	
AGR_L_M_4	N	20	0.02821	0.0357
	T	44	0.08992	

The plants at the northern limit flowered at the same time, had about the same seed weight and displayed the same increase of biomass compared to the transect plants.

Similarly, the comparison of sites close at the distribution boundary where *Hippocrepis* was growing (N) with sites where the species was lacking (O) revealed only few statistically significant differences

Table 5. Differences of site parameters between the northernmost grassland sites with (N) and without (O) occurrences of *Hippocrepis comosa*. Significant differences ($\alpha < 0.05$, according to the Kruskal-Wallis test) are marked in bold letters.

	N		O		
Parameter	Median	n	Median	n	Prob.
DEPTH_S	24.3	20	19.5	18	0.0955
AW_DEPTH	5411	18	4373	18	0.1288
AW_20CM	4584	18	3684	18	0.0818
PH	7.43	20	7.10	18	**0.0005**
ASPECT	75	20	143	18	**0.0004**
SLOPE	20	20	13	18	**0.0274**
HEIGHT_HL	55	20	53	18	0.8481
COVER_TL	0	20	0	18	0.3428
COVER_SL	0	20	0	18	**0.0069**
COVER_HL	83	20	90	18	**0.0013**
COVER_ML	45	20	10	17	**0.0017**
COVER_OG	5	20	5	18	0.8670
COVER_HC	10	20	0	18	**0.0001**
COVER_LI	18	20	10	18	0.4256

(Table 5). Cover of herb layer (COVER_HL) was significantly lower at sites with *Hippocrepis*, cover of moss layer (COVER_ML), pH of topsoil (PH), slope (SLOPE) and, of course, cover of *Hippocepis* were higher. The aspect of sites (ASPECT) was more oriented towards the South for the O than the N plots (Table 5). Among the microclimatic parameters, the O sites without *Hippocrepis* displayed neither unfavourable effective air temperature nor soil water content (Figure 5). When significant differences occurred, the O sites had higher effective temperatures (eT), higher potential direct PAR due to a more southern aspect and higher water content of soil (WC, except for WC in the last interval 7). No microclimatic reasons were found for the absence of this species.

Figure 7 shows the frost hardiness for different organs of *Hippocrepis comosa*. In comparison to the control, leaves, shoots and roots showed significant damage when exposed to temperatures of −18 °C or lower. Seedlings were already significantly damaged at −14 °C. Fitting the relative damage as a function of temperature and calculating the temperature at which 15% damage occurred revealed a ranking of frost sensibility (Figure 8). Most susceptible were seedlings, followed by leaves and roots. The shoots were the least sensitive organs. A damage of 50% was not found for any plant organ at temperatures higher than −25 °C.

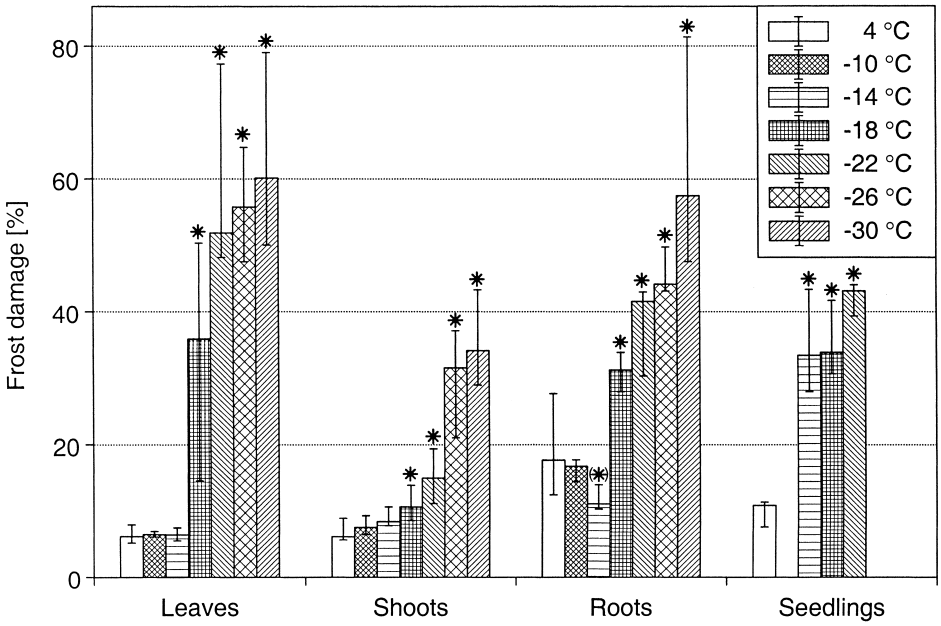

Figure 7. Frost damage to different plant organs and seedlings of *Hippocrepis comosa* in per cent of total damage by liquid nitrogen. Values are medians, error bars are upper and lower quartiles. For leaves, shoots and roots n = 10, for seedlings n = 5. * indicates significant differences between a certain treatment compared to the control (4 °C) according to the Kruskal-Wallis test. The α values were corrected by number of comparisons (α = 0.0083 for leaves, shoots and roots and 0.0167 for seedlings) to control the Type I experimentwise error. Please note that seedlings were treated with four temperatures only (+4 °C, −14 °C, −18 °C, −22 °C).

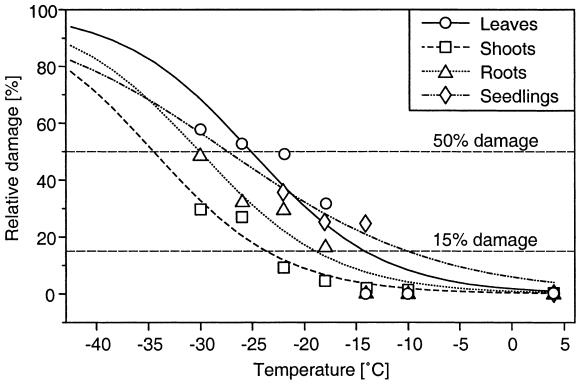

Figure 8. Relative damage to different plant organs and seedlings of *Hippocrepis comosa* as a function of temperature. 0% refers to the control (4 °C), 100% refers to the treatment with liquid nitrogen. Please note that seedlings were treated with four temperatures only (+4 °C, −14 °C, −18 °C, −22 °C).

The experiments on seedling establishment in the field revealed low germination rates of maximally 6.5% (Figure 9). Germination was observed during the whole investigation period with even some seeds germinating in July. The germination was lowest in the oat-grass meadow with only one germination event (E4) and highest in the chalk grassland plots (E1-E3). The rate of survival was remarkably high in all treatments with more than half of all seedlings surviving. The highest rate of survival with about 90% was found in open (E2) or fallow chalk grassland (E3); whereas in the oat-grass meadow (E4) only one emerged seedling survived. The germination rate on bare soil (E5) was only 50%. The microclimatic measurements revealed that survival was lower in plots with drier soils. At the end of observation period 3 the water content of the soil at plot E5 was down to 8%, whereas it was 12%, 18%, 25% and 32% in E1, E2, E4 and E3, respectively.

Discussion

The objective of the study was to relate a distribution boundary to microclimate on a regional scale. A main presupposition was the presence of a microclimatic gradient towards the distribution boundary of *Hippocrepis*. This assumption (hypothesis 1) proved to be valid; thus justifying the whole approach. However, this outcome could not have been expected from macroclimatic maps (Deutscher Wetterdienst 1964), which suggested no differences in the average annual temperatures along the transect. The mismatch is due (1) to inaccuracies of climatic maps, which are only interpolations based on general regressions to topog-

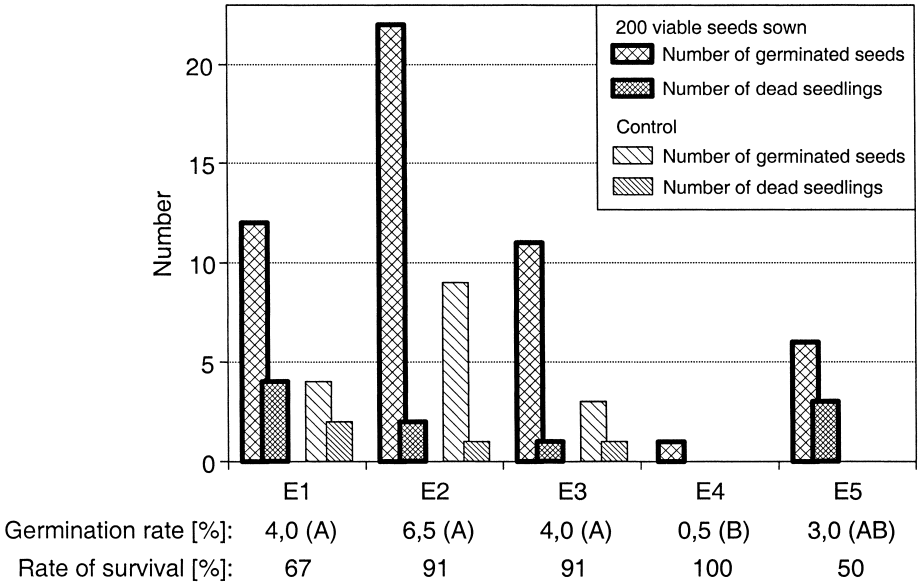

Figure 9. Germination rates and rates of seedling survival in 5 different vegetation structures. E1, mowed calcareous grassland; E2, open fallow grassland; E3, fallow grassland with bushes; E4, a yellow oat-grass meadow; E5, bare soil of a stony lithosol. Germination events were recorded either from the natural seed bank (control) or from additionally spread seeds (200 viable seeds sown). Different letters indicate statistically significant differences according to single comparisons subsequent to the Kruskal-Wallis test (after Conover in Bortz et al. (1990)).

raphy (Müller-Westermeier 1995), and (2) to the discrepancy in scale between macroclimate and microclimate (Geiger 1965; Stoutjesdijk and Barkman 1992).

Among the microclimatic parameters tested, temperature and radiation in particular are promising candidates for explaining the range limit of *Hippocrepis* because both parameters showed less favourable conditions towards the distribution boundary. In contrast, it is unlikely that the soil water content should be considered as a limiting factor because in our study it improved from south to north. The soil moisture gradient reflects the precipitation gradient within our study area for the investigation period. From April to July 1997 weather stations recorded 274 mm in the south (Göttingen) and 352 mm in the north (Hildesheim) (Deutscher Wetterdienst 1997). Furthermore, the investigation year 1997 reflects the long-term average from 1961 to 1990 with 236 mm in the south (Göttingen) and 300 mm in the north (Hildesheim) (Deutscher Wetterdienst 1997).

Our second objective was to relate growth to microclimate for various intervals. The regression analysis revealed a number of clear relationships between growth and microclimate especially for the first two observation intervals, in which the growth rates were positive. However, the method of ranking by correlation coefficient did not reveal a single, unequivocal factor explaining growth rates in all the intervals. This is a typical result of studies aiming at prediction of plant responses to environmental factors (Woodward 1992). Early in the growing season, vegetative growth was primarily positively related to soil temperature. This indicates that growth in this period may be limited by respiration rates for mobilization of stored carbohydrates from the roots. Another explanation is that mineralization rates in the soil are elevated and nutrient uptake is enhanced. From the end of May to middle of June the vegetative growth correlated best with soil water content, an indication that shoot growth is limited by water supply. This view is supported by the negative correlations in the same periods with radiation and air temperature, which are the driving force for evapotranspiration. Subsequently, vegetative growth ceased and flowering commenced. This antagonism between vegetative growth and flower formation, which has been observed in many plant species (Lang 1965), also seems to be effective in *Hippocrepis comosa*.

The correlation coefficients were comparably low but have a magnitude similar to those observed in other field studies (e.g. Wielgolaksi (1999)). The correlations appear to be satisfying when taking into account that all observations were made in the field where each replicated plot is exposed to a different set of interfering variables (Bruelheide 1999). Prob-

able interfering variables in the *Hippocrepis* study are nutrient supply, herbivores, competing neighbours, genetic constitution etc.; these factors account for the amount of unexplained variation in the example: with a regression coefficient of $r = 0.5$ ($r^2 = 0.25$) still 75% variation remains unexplained. This level of inaccuracy should be kept in mind when regressions are used to predict shifts in range limits (e.g. Huntley et al. (1995); Sykes and Prentice (1995); Iverson and Prasad (1998)).

Despite the existence of relationships between vegetative growth and microclimate, their contribution towards explaining the northern distribution boundary of *Hippocrepis* is very limited. None of the best correlating environmental variables in Table 3 showed a significant positive correlation with the distance from the distribution boundary in Table 2. Furthermore, no parameter of vegetative growth was found to correlate positively with distance. The insignificance of vegetative growth is also supported by the comparison of the northernmost sites with *Hippocrepis* occurrences with all of the transect sites (Table 4). Our study is not unique in failing to link vegetative growth in the field to distribution patterns. For example, Graves and Taylor (1986) showed that the altitudinal limit of *Geum urbanum* in Great Britain was not due to certain temperature requirements for vegetative growth. In contrast, Woodward and Pigott (1975) were able to predict the range limits of *Sedum rosea* and *S. telephium* from vegetative growth rates determined under field conditions and to confirm the predictions 15 years later (Woodward 1992).

Among the generative traits there was only one parameter, i.e. the percentage of set seeds, which showed both a positive correlation with distance from the distribution boundary and significant correlations with the air temperatures in the various intervals. The percentage of set seeds was remarkable with respect to its significant relation both positively and negatively to the same parameter, i.e. the effective air temperature at a height of 10 cm above ground (Fig. 6f and 6g). A high positive correlation was observed at the beginning of May, which may be an indication that high temperature promotes the development of ovules. This result is consistent with Fearn (1973) observation: "At its northern limit on Cronkley Fell, *H. comosa* has apparently not flowered for almost 40 years, and there are no records of it setting seed there." The pronounced effect of temperature on seed development, and consequently, on the production of mature seeds is also well known for many forest species, such as *Pinus sylvestris* and *Picea abies* (Almqvist et al. 1998) or *Picea mariana* (Sirois et al. 1999). Pigott and Huntley (1981) determined that seed sterility is the major cause of failure of *Tilia cordata* in north-west England due to temperatures insufficient for pollen-tube growth when pollination occurs. The negative correlation of seed setting with effective air temperature at the end of July can be interpreted as a sign that high air temperature hampers seed ripening, probably by affecting the water budget of the plant. This outcome is surprising especially for a species with submediterranean distribution. A general aspect of the antagonistic temperature effects in different parts of the growing season is that the widely used concept of accumulated temperatures resulting in growing degree days (e.g. Sykes and Prentice (1995); Diekmann (1996)) will probably fail to predict certain traits, such as seed setting.

Although not relevant for the range limit, the time of flowering was another trait that was related in an opposed manner to air temperature and soil moisture. We expected that flowering would be mainly dependent on temperature with high temperatures resulting in earlier flowering (Rathke and Lacey 1985; Diekmann 1996). Although such a relationship could be confirmed, its absolute correlation coefficient was much lower than for the water content of the soil. The latter may be an indication that flowering is retarded by moisture. Apart from photoperiod and temperature, moisture is one of the three major environmental cues for onset of flowering (Rathke and Lacey 1985). A plausible explanation would be that flower induction is stimulated when vegetative growth is inhibited – in the case of *Hippocrepis* by low soil moisture. As Borchert (1983) reported for some tropical trees, a diminished vegetative growth would result in high carbohydrate levels in the meristems, which could induce flower inition.

The strong influence of soil moisture on vegetative growth matches observations on the water status of *Hippocrepis comosa* during drought periods (Müller-Stoll 1936; Volk 1937). The species responds to even slight droughts with an immediate increase in water potential, a characteristic of euryhydric plants: they exhibit only limited stomatal regulation and tolerate large osmotic amplitudes (Larcher 1994). We observed some individuals that shed leaves and reduced the number of internodes during drought periods. In no case were these losses in biomass lethal; they solely indicate a strong drought tolerance. This fea-

ture probably contributes to the ability of *Hippocrepis comosa* to settle in mediterranean regions.

Although decreasing spring air temperatures may offer a possible explanation for the range limit by reducing seed setting, this parameter is by no means the only decisive factor for the occurrence of *Hippocrepis* on the regional scale. This was shown by the absence of significant differences between sites at the distribution boundary where *Hippocrepis* was growing versus those where it was absent (Table 5). Consequently, our third hypothesis that colonized sites were more favourable than non-colonized ones has to be rejected. *Hippocrepis comosa* can be expected to be able to grow at the investigated sites outside the present range. Most probably, it does not grow there because the seeds never reached these sites because there were no appropriate dispersal agents (compare Bonn and Poschlod (1998)). It is possible that the O sites lay outside the main paths of the wandering flocks of sheep. The question arises as to how far to the north the species can be expected to potentially grow without dispersal restrictions. From our results we expect that the species is able to grow at neighbouring sites outside the actual distribution range. Probably, *Hippocrepis* may be able to grow much further to the north. However, we did not design our study to address the question of the species' climatically potential range. For predictions on a broader scale the study would have had to adapt a longer transect, preferably on a continental scale as used in the IGBP transects (Koch et al. 1995; Steffen and Shvidenko 1996).

Another factor correlating well with distribution boundaries in many studies is frost (Iversen 1944; Hintikka 1963; Callauch 1986; Huntley et al. 1989, 1995; Woodward 1997). The experiments on frost hardiness of *Hippocrepis comosa* revealed significant damages at −18 °C or below, which is remarkably low for evergeen plants (Larcher 1994; Larcher and Bauer 1981). This value is even more remarkable as it was determined at the end of the winter season when frost hardiness is known to be decreasing (Till 1956; Kappen 1964; Larcher and Bauer 1981). In the study area, minimum temperatures below −18 °C are encountered only rarely (Deutscher Wetterdienst 1997); and, if they do, they are often mitigated by snow cover (Uemura 1989; Woodward 1997; Bruelheide 1999). Although seedlings are more sensible to frosts, they will not experience temperatures of less than −10 °C when they germinate in April or later in the growing season (Deutscher Wetterdienst 1997), which is the normal germination time. Consequently, frost susceptibility is not a probable reason for the northern distribution limit. Our fourth hypothesis that some life stages of *Hippocrepis comosa* might be particularly susceptible to frosts has to be rejected. Nevertheless, frost is a highly probable reason for the eastern distribution limit of *Hippocrepis comosa* where the species encounters colder winters with less precipitation. In field experiments transplanting the oceanic species *Euphorbia amygdaloides* and *Digitalis purpurea* beyond their eastern distribution boundary (Schulz and Bruelheide 1999; Bruelheide 1999), the combination of frost and snow cover appeared to be the key factor.

Our fifth objective was to relate seedling establishment to microclimate. The field experiments revealed that seedling survival is related to water content of the soil. Since water content increases towards the range boundary (Table 2), seedling establishment probably does not decline in this direction; this was confirmed by monitoring naturally emerged seedlings in some of the transect plots. Thus, seedling establishment cannot explain the northern distribution limit.

A factor that may be important for the southern rather than for the northern range limit might be germination ecology. The asynchronous germination in the establishment experiment possibly contributes to the drought tolerance of *Hippocrepis comosa*. The high variation in germination time may reflect unpredictable water supply conditions in spring and summer (Rathke and Lacey 1985). Either germination of *Hippocrepis* seeds is triggered by soil humidity and occurs only when soil moisture is high enough or it is just due to chance. In many legumes the germination of fresh seeds is inhibited by a hard seed coat (Baskin and Baskin 1989; Gardener et al. 1993). This form of primary dormancy is also apparent in the low germination rates observed for *Hippocrepis comosa*. With time the germination rate increases because of a softening of the seed coat (Newman 1965). The seed coat's role in inhibiting germination was also shown for *Hippocrepis comosa* (Hennenberg et al. in prep.). Softening of the testa is hastened by high constant temperatures and even more by daily alternating high and low temperatures (Quinlivan 1961). Consequently, those seeds whose testa is degraded to a sufficient degree would always germinate. A gradual rotting of the testa may even retard germination to subsequent years, which would present a bet-hedging strategy for interannual climatic variation.

The general conclusion of this study is that decreasing temperature, in particular air temperature, probably exerts the strongest influence on the northern distribution boundary of *Hippocrepis comosa* in Germany. It can be assumed that this factor affects generative reproduction more than vegetative growth. Air temperature does certainly not determine the distribution boundary by distinct threshold values but affects the production of viable seeds. In addition, air temperature is certainly not the only factor to be considered. It interferes with water supply in soils, which also seems to influence seed development, and even more importantly, probably is the key factor for seedling establishment. We consider it worthwhile to analyze in detail how water supply and air temperature affect seed production and seedling establishment during the vegetation period. However, such an analysis should be first performed in controlled environments and possible results should be tested in manipulative field experiments later.

Acknowledgements

We express our gratitude to M. Runge for all of his support in this project. We are especially grateful to G. Günter who contributed much help and knowledge in designing the study. Warm thanks also to all colleagues and the staff of the New Botanical Garden for their help in field and laboratory work and to D.F. Whybrew for the final polishing of the manuscript.

References

Almqvist C., Bergsten U., Bondesson L. and Eriksson U. 1998. Predicting germination capacity of *Pinus sylvestris* and *Picea abies* seeds using temperature data from weather stations. Can. J. For. Res. 28: 1530–1535.

Barkman J.J. 1977. Die Erforschung des Mikroklimas in der Vegetation: Theoretische und methodische Aspekte. In: Dierschke H. (ed.), Vegetation und Klima. Ber. Int. Symp. Int. Vereinig. Vegetationsk. Rinteln. Vaduz, Cramer, pp. 5–20.

Baskin J.M. and Baskin C.C. 1989. Physiology of dormancy and germination in relation to seed bank ecology. In: Leck M.A., Parker V.T. and Simpson R.L. (eds), Ecology of Seed Banks. Academic Press, London, pp. 53–66.

Bonn S. and Poschlod P. 1998. Ausbreitungsbiologie der Pflanzen Mitteleuropas: Grundlagen und kulturhistorische Aspekte. Quelle und Meyer, Wiesbaden.

Borchert R. 1983. Phenology and control of flowering in tropical trees. Biotropica 15: 81–89.

Bortz J., Lienert G.A. and Boehnke K. 1990. Verteilungsfreie Methoden in der Biostatistik. Springer, Berlin.

Box E.O., Crumpacker D.W. and Hardin D. 1993. A climatic model for location of plant species in Florida, USA. J. Biogeogr. 20: 629–644.

Bruelheide H. 1999. Experiments as a tool to investigate plant range boundaries. Verh. Ges. Ökol. 29: 19–26.

Bruelheide H. and Scheidel U. 1999. Slug herbivory as a limiting factor for the geographic range of *Arnica montana*. J. Ecol. 87: 839–848.

Callauch R. 1986. Die Frosthärte der Stechpalme (*Ilex aquifolium*). Verh. Ges. Ökol. 14: 523–527.

Deutscher Wetterdienst 1964. Klimaatlas von Niedersachsen.

Deutscher Wetterdienst 1997. Monatlicher Witterungsbericht, 45 (1–12).

Diekmann M. 1996. Relationship between flowering phenology of perennial herbs and meteorological data in deciduous forests in Sweden. Can. J. Bot. 74: 528–537.

Ellenberg H. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. 2nd ed. Scripta Geobotanica 18: 1–258.

Fearn G.M. 1972. The distribution of intraspecific chromosome races of *Hippocrepis comosa* L. and their phytogeographical significance. New Phytol. 71: 1221–1225.

Fearn G.M. 1973. Biological Flora of the British Isles. Hippocrepis comosa L. J. Ecol. 61: 915–926.

Fischer S.F., Poschlod P. and Beinlich B. 1995. Die Bedeutung der Wanderschäferei für den Artenaustausch zwischen isolierten Schaftriften. Beih. Veröff. Naturschutz Landschaftspfl. Bad.-Württ. 83: 229–256.

Fischer S.F., Poschlod P. and Beinlich B. 1996. Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. J. Appl. Ecol. 33: 1206–1222.

Gardener C.J., Mc Ivor J.G. and Jansen A. 1993. Passage of legume and grass seeds through the digestive tract of cattle and their survival in faeces. J. Appl. Ecol. 30: 63–74.

Garve E. 1993. Rote Liste der gefährdeten Farn- und Blütenpflanzen in Niedersachsen und Bremen, 4th ed. Informationsd. Natursch. Niedersachs. 13: 1–37.

Garve E. 1994. Atlas der gefährdeten Farn- und Blütenpflanzen in Niedersachsen und Bremen. Kartierung 1982-1992. Naturschutz Landschaftspfl. Nieders. 30: 1–478.

Geiger R. 1965. The Climate Near the Ground. Harvard University Press, Cambridge.

Good R. 1964. The Geography of the Flowering Plants. 3rd edn. Longmans, London.

Grace J. 1987. Climatic tolerance and the distribution of plants. New Phytol. 106 : 113–130.

Graves J.D. and Taylor K. 1986. A comparative study of *Geum rivale* L. and *G. urbanum* L. to determine those factors controlling their altitudinal distribution. I. Growth in controlled and natural environments. New Phytol. 104: 681–691.

Greene D.F. and Johnson E.A. 1989. A model of wind dispersal of winged or plumed seeds. Ecology 70: 339–347.

Harper J.L. 1977. Population Biology of Plants. Academic Press, London.

Hegi G. 1924. Illustrierte Flora von Mittel-Europa. Part 3. 1st edn. Vol. 4. Parey, Berlin.

Hintikka V. 1963. Über das Grossklima einiger Pflanzenareale in zwei Klimakoordinatensystemen dargestellt. Ann. Bot. Fenn. 34 : 1–64.

Holten J.I. 1993. Potential effects of climatic change on distribution of plant species, with emphasis on Norway. In: Holten J.I., Paulsen G. and Oechel W.C. (eds), Impacts of Climatic Change on Natural Ecosystems, with Emphasis on Boreal and Arctic/Alpine Areas. Norwegian Institute for Nature Research (NINA), Trondheim, pp. 84–104.

Huntley B., Bartlein P.J. and Prentice I.C. 1989. Climatic control of the distribution and abundance of beech (*Fagus* L.) in Europe and North America. J. Biogeogr. 16: 551–560.

Huntley B., Berry P.M., Cramer W. and McDonald A.P. 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces. J. Biogeogr. 22: 967–1001.

Hunt R. 1989. Basic Growth Analysis. Unwin Hyman, London.

Iversen J. 1944. *Viscum*, *Hedera* and *Ilex* as climate indicators. Geol. Fören. Förhandl. 66 : 463–483.

Iverson L.R. and Prasad A.M. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecol. Monogr. 68: 465–485.

Jäger E.J. 1972. Comments on the history and ecology of continental European plants. In: Valentin D.H. (ed.), Taxonomy, Phytogeography and Evolution. Academic Press, London, pp. 349–362.

Jäger E.J. 1990. Pflanzenarealgrenzen als Leistungsgrenzen. Biol. Rundsch. 28: 295–306.

Jäger E.J. 1995. Klimabedingte Arealveränderungen von anthropochoren Pflanzen und Elementen.der natürlichen Vegetation. Angew. Landschaftsökol. (Bonn-Bad Godesberg) 4: 51–57.

Jalas J. and Suominen J. (eds) 1972–1991. Atlas Florae Europaeae. Societas Biologica Fennica Vanamo, Helsinki.

Jones H.G. 1983. Plants and Microclimate. Cambridge Univ. Press, Cambridge.

Kappen L. 1964. Untersuchungen über den Jahreslauf der Frost-, Hitze- und Austrocknungsresistenz von Sporophyten einheimischer Polypodiaceae (Filicinae). Flora 155: 123–166.

Kirchner O., Loew E., Schröter C. and Wangerin W. 1938. Lebensgeschichte der Blütenpflanzen Mitteleuropas. Vol. III. Ulmer, Stuttgart.

Koch G.W., Vitousek P.M., Steffen W.L. and Walker B.H. 1995. Terrestrial transects for global change research. Vegetatio 121: 53–65.

Lang A. 1965. Physiology of flower initiation. In: Ruhland W. (ed.), Encyclopedia of Plant Physiology. Springer, Berlin, pp. 1380–1536.

Larcher W. and Bauer H. 1981. Ecological significance of resistance to low temperature. In: Lange O.L., Nobel P.S., Osmond C.B. and Ziegler H. (eds), Physiological Plant Ecology. I. Encyclopedia of Plant Physiology 12 A. Springer, Berlin, Heidelberg, pp. 403–437.

Larcher W. 1994. Ökophysiologie der Pflanzen. Leben, Leistung und Streßbewältigung der Pflanzen in ihrer Umwelt. 5th edn. Ulmer, Stuttgart.

Meusel H. and Buder J. 1955. Verbreitungskarten mitteldeutscher Leitpflanzen. 8. Reihe. Wiss. Z. Martin-Luther-Univ. Halle 5: 297–334.

Meusel H., Jäger E. and Weinert E. 1964. Vergleichende Chorologie der zentraleuropäischen Flora. Vol. 1. Karten. Gustav Fischer, Jena.

Müller-Westermeier G. 1995. Numerische Verfahren zu Erstellung klimatologischer Karten. Ber. Dt. Wetterdienst 193: 1–18.

Müller-Stoll R. 1936. Ökologische Untersuchungen an Xerothermpflanzen des Kraichgaus. Z. Bot. 29: 161–253.

Murray M.B., Cape J.N. and Fowler D. 1989. Quantification of frost damage in plant tissues by rates of electrolyte leakage. New Phytol. 113: 307–311.

Newman E.I. 1965. Factors controlling the germination date of winter annuals. J. Ecol. 51: 625–638.

Oberdorfer E. 1978. Süddeutsche Planzengesellschaften. Teil II. Gustav Fischer, Stuttgart.

Pigott C.D. and Huntley J.P. 1978. Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. I. Distribution in north-west England. New Phytol. 81: 429–441.

Pigott C.D. and Huntley J.P. 1980. Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. II. History in north-west England. New Phytol. 84: 145–164.

Pigott C.D. and Huntley J.P. 1981. Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. III. Nature and causes of seed sterility. New Phytol. 87: 817–839.

Poschlod P. and Jackel A.K. 1993. Untersuchungen zur Dynamik von generativen Diasporenbanken von Samenpflanzen in Kalkmagerrasen. Flora 188: 49–71.

Poschlod P., Kiefer S., Tränkle U., Fischer S. and Bonn S. 1998. Plant species richness in calcareous grasslands as affected by dispersability in space and time. Appl. Veg. Sc. 1: 75–90.

Poschlod P., Matthies D., Jordan S. and Mengel C. 1996. The biological flora of Central Europe – an ecological bibliography. Bull. Geobot. Inst. ETH 62: 89–108.

Quinlivan B.J. 1961. The effect of constant and fluctuating temperatures on the permeability of the hard seeds of some legume species. Aust. J. Agric. Res. 12: 1009–1022.

Rathke B. and Lacey E.P. 1985. Phenological patterns of terrestrial plants. Ann. Rev. Ecol. Syst. 16: 179–214.

Saetersdal M. and Birks H.J.B. 1997. A comparative ecological study of Norwegian mountain plants in relation to possible future climatic change. J. Biogeogr. 24: 127–152.

SAS Institute 1987. SAS/STAT Guide for Personal Computers. Ver. 6., Cary, NC.

SAS Institute 1989. SAS Procedures Guide, Release 6.03., Cary, NC.

Sauer R.H. 1976. The relationship of cumulative sums and moving averages of temperatures to reproductive phenology in Clarka. Am. Midl. Nat. 95: 144–158.

Scheidel U. and Bruelheide H. 1999. Selective slug grazing on montane meadow plants. J. Ecol. 87: 828–838.

Schulz C. and Bruelheide H. 1999. An experimental study on the impact of winter temperature on the distribution of *Euphorbia amygdaloides* L. in Central Germany. In: Klötzli F. and Walther G.R. (eds), Recent Shifts in Vegetation Boundaries of Deciduous Forests, Especially Due to General Global Warming. Birkhäuser, Basel, pp. 121–150.

Sirois L., Bégin Y. and Parent J. 1999. Female gametophyte and embryo development of black spruce along a shore-hinterland climatic gradient of a recently created reservoir, northern Quebec. Can. J. Bot. 77: 61–69.

Söyrinki N. 1954. Vermehrungsökologische Studien in der Planzenwelt der Bayerischen Alpen. Ann. Bot. Soc. Zool. Bot. Fennicae Vanamo 27: 1–232.

Steffen W.L. and Shvidenko A.Z. 1996. IGBP northern Eurasia study: prospectus for an integrated global change research project. IGBP Global Change Rep. 37: 1–95.

Stender S., Poschlod P., Vauk-Hentzelt E. and Dernedde T. 1997. Die Ausbreitung von Pflanzen durch Galloway-Rinder. Verh. Ges. Ökol. 27: 173–180.

Steponkus P.L. and Lanphear F.O. 1967. Refinement of the triphenyl tetrazolium chloride method of determining cold injury. Plant Physiol. 42: 1423–1426.

Steubing L. and Fangmeier A. 1992. Pflanzenökologisches Praktikum. Ulmer, Gießen.

Stoutjesdijk P. and Barkman J.J. 1992. Microclimate, Vegetation and Fauna. Opulus Press, Knivsta.

Sykes M.T. and Prentice I.C. 1995. Boreal forest futures: modelling the controls on tree species range limits and transient responses to climate change. Water Air Soil Pollution 82: 415–428.

Tan K.H. 1996. Soil Sampling, Preparation and Analysis. Marcel Decker, Georgia, USA.

Thompson K., Bakker J.P. and Bekker R.M. 1997. The Soil Seed Banks of North West Europe: Methodology, Density and Longevity. Cambridge Univ. Press, Cambridge.

Till O. 1956. Über die Frosthärte von Pflanzen sommergrüner Laubwälder. Flora 143: 499–542.

Uemura S. 1989. Snowcover as a factor controlling the distribution and speciation of forest plants. Vegetatio 82: 127–137.

Urbanska K.M. 1997. Safe sites- interface of plant population ecology and restoration ecology. In: Urbanska K.M., Webb N.R. and Edwards P.J. (eds), Restoration Ecology and Sustainable Development. Cambridge University Press, Cambridge, pp. 81–110.

Volk O.H. 1937. Untersuchungen über das Verhalten der osmotischen Werte von Pflanzen aus steppenartigen Gesellschaften und lichten Wäldern des mainfränkischen Trockegebietes. Z. Bot. 32: 65–149.

Wagner S. 1995. Übertragung strahlungsrelevanter Wetterinformation aus punktuellen PAR-Sensordaten in größere Versuchsflächenanlagen mit Hilfe hemisphärischer Fotos. Allg. Forst- und Jagd-Zeitung 167: 34–40.

Walter H. and Straka H. 1970. Arealkunde (Floristisch-historische Geobotanik). 2nd edn. Ulmer, Stuttgart.

Wielgolaksi F.-E. 1999. Starting dates and basic temperatures in phenological observations of plants. Int. J. Biometeorol. 42: 158–168.

Woodward F.I. 1987. Climate and Plant Distribution. Cambridge Univ. Press, Cambridge.

Woodward F.I. 1992. Tansley Review No. 41. Predicting plant responses to global environmental change. New Phytol. 122: 239–251.

Woodward F.I. 1997. Life at the edge: a 14-year study of a *Verbena officinalis* population's interaction with climate. J. Ecol. 85: 899–906.

Woodward F.I. and Pigott C.D. 1975. The climatic control of the altitudinal distribution of *Sedum rosea* (L.) Scop. and *S. telephium* L. I. Field observations. New Phytol. 74: 323–334.