

Translocation of a montane meadow to simulate the potential impact of climate change

Bruelheide, Helge

Albrecht-von-Haller-Institute for Plant Sciences, Department of Ecology and Ecosystem Research, Untere Karspüle 2, D-37073 Göttingen, Germany; Fax +49551393556; E-mail hbruelh@gwdg.de

Abstract. The effects of warming on a montane meadow was simulated by a translocation experiment. A coherent piece of turf and soil was transferred from 600 m to 170 m a.s.l., corresponding to an increase in temperature of ca. 2.8 K. The vegetation was monitored by recording cover and counting individuals one year before the translocation and continued for the subsequent seven years. For comparison, a control plot that had also been translocated but remained at 600 m was monitored. Four of eight species with a montane distribution in Europe showed a constant degree of cover during the investigation period (*Nardus stricta*, *Poa chaixii*, *Polygonatum verticillatum*, *Potentilla erecta*). In contrast, another four montane species declined in cover or died out (*Arnica montana*, *Meum athamanticum*, *Hypericum maculatum*, *Galium harcynicum*). None of these species declined on the control plot. It is argued that the species' responded individually to the site factors that had changed with the translocation to low altitude. A direct effect of enhanced temperature was probably the reason for the decline of only one species (*Meum athamanticum*). Reduced humidity might be the reason for the extinction of two moisture demanding species (*Viola palustris*, *Succisa pratensis*). The biomass of the plot increased by increased growth of one of the matrix species (*Festuca rubra*), probably due to elevated nutrient mineralization. Many low growing species responded indirectly to the reduced light availability, caused by an increased level of competition for light (e.g. *Galium harcynicum*). Increased slug herbivory at low altitude resulted in the extinction of *Arnica montana*. At the end of the investigation period, the similarity in species composition to the initial state was only 45%, indicating that the community had changed into a different plant association. The importance of considering biotic interactions when predicting the impacts of climate change is discussed.

Keywords: Global warming; Herbivory; Mountain plant; Permanent plot; Plant community.

Nomenclature: Phanerogams according to Ehrendorfer (1973); mosses according to Frahm & Frey (1987).

Abbreviations: AFE = Atlas Florae Europaeae; RGR = Relative growth rate.

Introduction

There are many approaches used to predict the impact of climatic change on plant distribution. Many theories of how geographical ranges will shift with climatic warming are based on correlations between present day distribution of plants and long-term climatic parameters (e.g. Jäger 1972; Meusel & Jäger 1989; Box et al. 1993; Saetersdal & Birks 1997). Using these relationships to calculate climatic envelopes, plant ranges can be extrapolated according to different scenarios of changing temperature or humidity (Holten 1993; Jäger 1995; Huntley et al. 1995; Iverson & Prasad 1998). A disadvantage of these predictions is that they are purely correlative and thus include some pitfalls. For example, Huntley et al. (1995) found the distribution of many European species to be limited by three parameters, mean temperature of the coldest month, temperature sum above a 5 °C threshold and the estimated ratio of actual to potential evapotranspiration. Taking *Tilia cordata* as an example, a combination of these parameters allowed simulation of the observed occurrences in the 50-km grid cells of the Atlas Florae Europaeae (AFE) with an accuracy of 81.9%. Even the gap with absences of *T. cordata* in the AFE cells in Belarus and westernmost Russia is simulated although this is certainly an artefact due to incomplete data (compare the map in Meusel et al. 1978, p. 281). The gap is retained in all scenarios of climatic warming and is shifted north-eastwards. This example is not put forward to question the correlative approach in general but to warn against mistaking correlations for causalities. The underlying operating mechanisms can only be discovered by studies on the species in question. Pigott & Huntley (1978, 1980, 1981) found that low summer temperatures do not allow an adequate pollen tube growth rate in *T. cordata*; this results in a failure to fertilize the ovary within the life span of the pollen tube.

The ultimate answer of how a given species will actually respond to a modified climate can only be determined by field experiments that include biotic interactions with other species. For example, the level of

competition may change with differing neighbour plants or changes in productivity (Rochow 1970; Woodward & Pigott 1975). In the case of single species, individuals can easily be translocated along climatic gradients (Bruelheide 1999). This has been successfully performed for alpine *Carex* species (Wagner & Reichegger 1997), alpine meadow species (Volkova et al. 1999), montane and oceanic species (Bruelheide & Lieberum 2001; Bruelheide & Heinemeyer 2002) and *Eucalyptus* species (Prober 1992). The translocation of a whole community is much more difficult because of the inherent logistic problems. In this study, the opportunity to perform such an experiment arose by chance when a montane meadow had to be translocated for the building of a bypass road around Braunlage in the Harz Mountains. There was a large investment of time and money in the project because the meadows were rich in species threatened in Lower Saxony (Garve 1993; Bruelheide et al. 1997). The project included a special translocation technique to minimize disturbance effects and an efficiency control for 5 yr (Bruelheide & Flintrop 1999, 2000). Although the main objective was to preserve as much meadow as possible, a small fragment could be removed from the project and moved to a lower altitude. It is the objective of this study to report the development of the community over the following seven years. The main hypothesis was that the climatic conditions at the lower altitude would be disadvantageous for montane species and would favour widespread species.

Methods

Study site

The study site is located on a meadow covered plateau south of Braunlage (Lower Saxony; 600 m a.s.l.; N 41°42,88' E 010°37,10') in the Harz Mountains. In the corridor affected by the road works four different vegetation types were distinguished (Bruelheide & Flintrop 2000). The plots that were translocated in this study were selected on the basis of a detailed vegetation map at the scale 1:500 (Bruelheide, Flintrop & Seifert unpubl.). According to reference relevés at the study site (Bruelheide & Flintrop unpubl.), the plots are typical of the *Arnica* type, a species-rich mat-grass community (*Polygalo-Nardetum* according to Peppler 1992). Apart from *Arnica montana*, characteristic species for this community are indicators of oligotrophic conditions, such as *Nardus stricta* (matt-grass), *Avenella flexuosa*, *Veronica officinalis* and *Galium harcynicum*, but also meadow species such as *Veronica chamaedrys*, *Leucanthemum vulgare* and *Ranunculus acris* (Table 1). This vegetation type was mainly found on mounds

that represented outcrops of the diabase bedrock. The soils were very stony, reaching a stone content of 80 vol.% at a depth of 0.5 m, and had a pH between 5.0 and 6.0 in the Ah horizon.

Translocation and monitoring

The study started with the selection of two plots (2 m × 2 m) in 1992, one year before translocation. The corners of the quadrats were marked with magnets (see Bruelheide 1995, p. 25) that allowed for determination of their exact position using a metal detector. The magnets remained in the soil during the translocation procedure. In June 1993, the two plots were translocated in two pieces each 2 m long, 1 m wide, 0.5 m deep and weighing ca. 1.5 t, with a special front-end shovel attached to a bulldozer (Bruelheide & Flintrop 1999, 2000). Gaps which arose during the translocation were filled with subsoil. These areas of bare soil covered ca. 10% of the surface area. One plot served as control for assessing the disturbance effect of the translocation and was transferred with the bulldozer directly to the nearby receptor area at the same altitude (hereafter referred to as the plot at 600 m), together with a total of 4186 m² of meadows that were removed from the road corridor. The other plot was put on a lorry and moved to the Experimental Botanical Garden in Göttingen where it was integrated in the Alpinum at 170 m a.s.l. (in the following referred to as the plot at 170 m). The new location had a slightly southern aspect (5° SSE) compared to the donor site (0°). The receptor site was prepared by excavating a square pit 2.25 m × 2.25 m to a depth of 0.5 m and removing a 2-m strip of vegetation around it. The edge of the pit was filled with subsoil (palaeozoic diabase) and covered with additional turf strips from the donor site.

The cover of all phanerogams and mosses in the plots was recorded annually in June or early July by the author from 1993 to 1999 using a modified Londo scale (see Table 1). In addition, individuals were counted when less than 20 individuals of a species were present. Exceptions were some threatened species including *Arnica montana*, *Dianthus deltoides* and *Rhinanthus minor* whose individuals were always counted. Shoots were counted for most species although rosettes were counted for *Arnica montana*, *Succisa pratensis*, *Carex pilulifera* and *Cardaminopsis halleri* and single leaves for *Meum athamanticum* and *Viola palustris*.

Table 1. cont.

Year	Translocated from 600 to 170 m a.s.l.								Translocated from 600 to 600 m a.s.l.							
	92↓	93	94	95	96	97	98	99	92↓	93	94	95	96	97	98	99
•							r ¹	+								
•							r ¹	r ²								
•							r ¹	r ²								
•							r ¹	r ¹								
7.	=								r ⁵	r ⁹	r ¹⁵	r ¹⁰	r ³	r ⁸	r ⁹	r ⁴
=									r ¹	r ²	r ²	r ⁵	r ⁴	r ⁴	r ⁵	r ⁶
↗									+	+	#	#	r ³³	+	+	+
↑									r ³	r ¹²	r ¹³	r ⁷	r ⁸	r	r	r
↑									r ⁴	r ¹¹	r ²²	+ ⁵²	+ ⁶⁶	+	+	+
•										r			r	r	r ¹	r ¹
•										r ¹	r ¹				r ¹	
•											r		r ¹			

Further species occurred only in one year at 170 m: in 1997: *Stellaria media* r², *Vicia hirsuta* r²; in 1998: *Barbula* sp. r, *Cirsium arvense* r, *Fraxinus excelsior* r¹, *Taraxacum officinale* r³; in 1999: *Acaulon muticum* r, *Arenaria serpyllifolia* r³, *Betula pendula* r¹, *Bromus hordeaceus* r¹, *Calligonella cuspidata* r, *Galium aparine* r, *Hieracium* sp. r¹, *Valerianella* sp. r³, *Veronica arvensis* r¹; in the plot at 600 m in 1993: *Poa pratensis* r¹; in 1995: *Leontodon autumnalis* r¹. ¹ incl. *Ditrichum heteromallum*, ² incl. *Brachythecium albicans*;

= = Constant cover during the study period or changing by only 1 cover class; ↓ = Continuously decreasing cover of at least 2 cover classes or a pronounced decrease in number of individuals; ↗ = Intermittent increase in cover or number of individuals but turning back to initial values; ↑ = Continuously increasing cover of at least two cover classes or a pronounced increase in number of individuals; † Decreasing until extinct; • = New establishment.

Design limitations

Although eight plots were translocated at 600 m (Bruelheide & Flintrop unpubl.), only one plot was transferred to 170 m. Among the eight plots at 600 m the plot with the most similar initial species composition was chosen for comparison with the plot at 170 m. The comparison of only two plots involves severe design limitations because it does not allow statistical tests of significant treatment differences. Nevertheless, the experiment was deliberately carried out without replicates. A replication with more 2 m × 2 m plots was not possible because the meadow fragment available for this experiment was only ca. 6 m² in size. Even this size raised problems because this vegetation type is protected by law. Although it would have been possible to divide the available turf area into smaller pieces it would have been necessary to transfer these small pieces to independent target locations for appropriate statistical design. This procedure would have involved much larger edge effects (8 m edge with one piece compared to 20 m with six pieces). Such edge effects are responsible for the failure in many translocation studies because species with runners at the receiving sites intrude the translocated sections shortly after translocation (Klötzli 1978; Worthington & Helliwell 1987). Because the aim of the

study was to monitor community change manual weeding was excluded. To minimize the invasion of weeds existing vegetation was removed at the receptor location. Under these conditions small grassland patches would have experienced very different microclimatic conditions compared to closed turfs. Below-ground edge effects were also problematic because of different bedrock (Lower Muschelkalk of European Triassic). Consequently, I decided to leave the turf in one piece and accepted the drawback of lacking replicates.

Initially, further control plots that were undisturbed had been established in 1992 in the surrounding meadows at the donor site. These plots had to be given up in 1994 because in 1993 the local farmer had ignored the nature conservation regulations and had applied a strong fertilizer treatment with manure. In consequence, these grasslands developed into a much more productive vegetation type than all translocated plots.

Climatic conditions

The long-term annual mean temperatures are 8.5 °C in Göttingen (170 m) and 5.8 °C in Braunlage (600 m), annual precipitation is 607 mm and 1234 mm, respectively (Walter & Lieth 1967; Glässer 1994). Based on observations of the official weather stations from 1992

to 1999 (Anon. 1992-1998, 1999), regressions for monthly mean temperatures (T) and monthly precipitation (P) yield the equations $T_{\text{Gött.}} = 0.9878 \cdot T_{\text{Braun.}} + 2.8562$ and $P_{\text{Gött.}} = 0.3129 \cdot P_{\text{Braun.}} + 20.086$, respectively ($n = 96$). During the investigation period the monthly mean temperatures were ca. 2.8 K higher in Göttingen than in Braunlage and monthly precipitation was ca. three times higher in Braunlage than in Göttingen. The difference in temperature is within the range of increase that is predicted for this part of Europe. Using nine different general circulation models, climate warming at time of CO₂ doubling north of 50° N is predicted to be between 1.0 and 4.5 K in summer and 2.5 to 4.5 in winter (Houghton et al. 1996).

Data analysis

The change in species composition of each plot with respect to the initial stage in 1992 was evaluated by calculating the similarity index recommended by van der Maarel (with the Mulva 4.0 package; Wildi & Orlóci 1990):

$$\text{Similarity} = \frac{\sum x \cdot y}{\sum x^2 + \sum y^2 + \sum x \cdot y} \quad (1)$$

with x and y being percentage cover of a species in the two relevés compared. To analyse the floristic change, a correspondence analysis (CA) was calculated. The analysis was performed with CANOCO 4.0 (ter Braak & Šmilauer 1998) which has been corrected to avoid the instability reported by Oksanen & Minchin (1997). For all types of analyses the cover of the species was used by taking the class means of the Londo scale.

Seed bank analysis

Soil samples were taken on the 02.04.1997 from one of the plots that had been translocated at 600 m. Twelve samples were taken from the topsoil (0-12 cm) over a 12-m² area. In total, an area of 1452 cm² was sampled representing 1.21% of the 12 m². Emerging seedlings were continuously counted and then removed. The observations were continued until September 1997.

Results

Cover and number of individuals of all species are shown in Table 1. The species are arranged in the sequence of their tendency (1) to maintain constant cover in the plot translocated to 170 m during the study period, (2) to increase in cover or number, (3) to decrease in cover, (4) to become extinct but then to re-establish themselves, (5) to become definitely extinct

and (6) to establish themselves anew in the plots. Group 6 is divided into the species that were found regularly at 600 m, which is reflected by their presence in the control plot (6a), and those that were not (6b). Group 7 comprises the species only found in the control plot. For comparison, the tendency to decrease, increase or maintain constant cover is also given for the control plot at 600 m (Table 1, col. 2). There are a few species that were common in the whole translocation area but did not occur in the control plot. For these species the tendency is based on Bruelheide & Flintrop (2000). In the following, indicator values and life form refer to Ellenberg et al. (1992), abbreviated as T_{iv} for temperature, F_{iv} for moisture, R_{iv} for soil pH and N_{iv} for nitrogen supply indicator values. Life history, established strategy (C = competitive, S = stress-tolerant, R = ruderal), seed bank type and agency of dispersal refer to Grime et al. (1988). Data on the geographical distribution of species were taken from Meusel et al. (1965, 1978) and Meusel & Jäger (1992).

Most species with an initial cover greater than 10% maintained constant cover during the investigation or changed by only one cover class (Table 1, group 1). The main floristic components of mat-grass swards belong to this group, such as *Nardus stricta*, *Agrostis tenuis*, *Luzula campestris* and *Rhytidiadelphus squarrosus*. The phanerogams are characterized by an S- or CSR-strategy and R_{iv} and N_{iv} of ≤ 4 . The slight increase of *Polygonum bistorta*, one of the three vascular plants that indicate soil moisture ($F_{\text{iv}} \geq 7$) is noteworthy. Apart from *N. stricta*, montane species in this group are *Poa chaixii*, which slightly increased in cover, and *Polygonatum verticillatum*, which decreased in number but was never frequent in the control plot or in other meadow plots at 600 m (Bruelheide & Flintrop 2000).

The group of species that increased in cover (group 2) also consists mainly of species typical of mat-grass swards, i.e. *Festuca rubra*, *Anthoxanthum odoratum*, *Veronica officinalis* and *Potentilla erecta*. The increase in cover of *P. erecta* is remarkable because the species primarily occurs at montane altitudes. An exception is *Rumex acetosa* which is an indicator of better nutrient supply ($N_{\text{iv}} = 6$). At 170 m *F. rubra* contributed most to the biomass, evidenced by an increase in height and cover of the herb layer (see Table 1). In the control plot none of these species showed a comparable increase; *Galium harcynicum* increased in cover, taking advantage of the new created gaps by spreading from the edges of the turves. In contrast, at 170 m the gaps were smaller and were successively occupied by various species.

In total, 17 species declined after translocation to 170 m (Table 1, groups 3, 4 and 5). They do not differ from species with constant or increasing cover with regard to life form and established strategy. The vascular

Table 2. Species found in the seedbank. The number of germinated seeds refer to an area of 1452 cm² and a soil depth of 12 cm.

Species	Germinated seeds
<i>Agrostis tenuis</i>	582
<i>Anthoxanthum odoratum</i>	3
<i>Avenella flexuosa</i>	2
<i>Campanula rotundifolia</i>	2
<i>Carex leporina</i>	3
<i>Festuca rubra</i>	1
<i>Galium hircynicum</i>	100
<i>Hieracium laevigatum/lachenalii</i>	2
<i>Hypericum maculatum</i>	327
<i>Lathyrus linifolius</i>	1
<i>Luzula campestris</i>	38
<i>Meum athamanticum</i>	1
<i>Polygonum bistorta</i>	1
<i>Potentilla erecta</i>	3
<i>Rubus fruticosus</i>	1
<i>Rumex acetosa</i>	1
<i>Silene dioica</i>	37
<i>Taraxacum officinale</i>	6
<i>Trifolium repens</i>	1
<i>Tussilago farfara</i>	1
<i>Veronica officinalis</i>	76
<i>Viola tricolor</i>	1

plants are hemicryptophytes or chamaephytes and have an S- or CSR-strategy. Some of the declining species are restricted to montane altitudes, i.e. *Meum athamanticum*, or are much more frequent there, i.e. *Arnica montana*, *Hypericum maculatum* and *Galium hircynicum*. Their montane distribution is reflected with $T_{iv} \geq 5$. *M. athamanticum*, which was the dominant herbaceous plant species in the stands, was observed to grow less vigorously in the year after the translocation and to produce no flowering shoots. In the following year the species died out. The extinction of all but one individual of *A. montana* in the year after the translocation was at least partly caused by slugs, which were abundant in the New Botanical Garden and, on the plot, preferred to feed on *A. montana* leaves. The last *A. montana* individual was eaten by slugs on the 09.06.1994, when the vegetation on the plot was recorded.

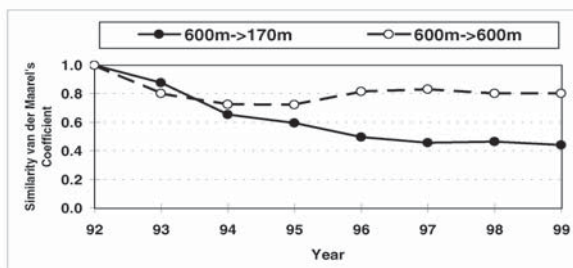


Fig. 1. Similarity in species composition of the plot translocated to 170 m and the control plot at 600 m with regard to their initial state before translocation (1992), using percentage cover and van der Maarel's similarity coefficient.

Hypericum maculatum and *Galium hircynicum* (group 4) stand out from the other species by first declining until they became extinct two years after the translocation and then re-establishing from seed. Both species are known to have a large persistent soil seed bank (seed bank type 4; Grime et al. 1988). This conforms with the seed bank analysis (Table 2), where *H. maculatum* and *G. hircynicum* are the second and third most abundant species that emerged from the seed bank. However, other species that occurred in the seed bank experiment or that are known to have a persistent seed bank did not re-establish, i.e. *Hieracium laevigatum*, *Vaccinium myrtillus*, *Campanula rotundifolia* and *Carex pilulifera*.

Among the extinct species (group 5), there are two which are characterized by high moisture demands, i.e. *Viola palustris* ($F_{iv} = 9$) and *Succisa pratensis* ($F_{iv} = 7$). Other species that died out are some typical mosses of mat-grass swards, i.e. *Dicranum scoparium*, *Pleurozium schreberi* and *Polytrichum formosum*.

The newly established phanerogams (group 6a) have probably been translocated with the seed bank (*Dianthus deltoides*, *Rhinanthus minor* and *Cardaminopsis halleri*), although they were not found in the seed bank experiment (Table 2), probably because of their rarity. The mosses *Dicranella heteromalla* and *Pohlia nutans* are ubiquitous species on newly exposed bare soil.

Most species of group 6b are not native to montane meadows but are common lowland weeds that are abundant in the New Botanical Garden such as *Bromus sterilis*, *Geranium dissectum*, *Epilobium spec.*, *Trifolium dubium*, *Vicia angustifolia* and *V. tetrasperma*. They are all therophytes, indicators of high temperatures ($T_{iv} = 6$), intermediate levels of nitrogen supply ($N_{iv} = 5$) and ruderals (R). Some other new established species are characterized by a C-, CR- or CSR-strategy, i.e. *Agropyron repens*, *Dactylis glomerata*, *Holcus lanatus*, *Sonchus arvensis*, *Trifolium repens*, *Convolvulus arvensis* and *Cerastium holosteoides*. The last two species, in particular, could spread considerably following establishment. Some species that appeared in the final year of observation are characteristic nitrogen indicators, i.e. *Stellaria media* and *Galium aparine* (both with $N_{iv} = 8$).

The shift in species composition compared to the initial state of each plot in 1992 is shown in Fig. 1. The translocation had also a marked effect on the control plot at 600 m, indicated by a decreasing similarity to ca. 70% to the initial stand. From 1996 onwards the vegetation recovered and attained a constant similarity of ca. 80%. In contrast, the plot translocated to 170 m is characterized by a continuously decreasing similarity to 45.7% in 1997. Although many new species appeared in the plot in the last three observation years (Table 1), the similarity between this plot and the initial state remained almost unchanged. This is due to the constant cover of

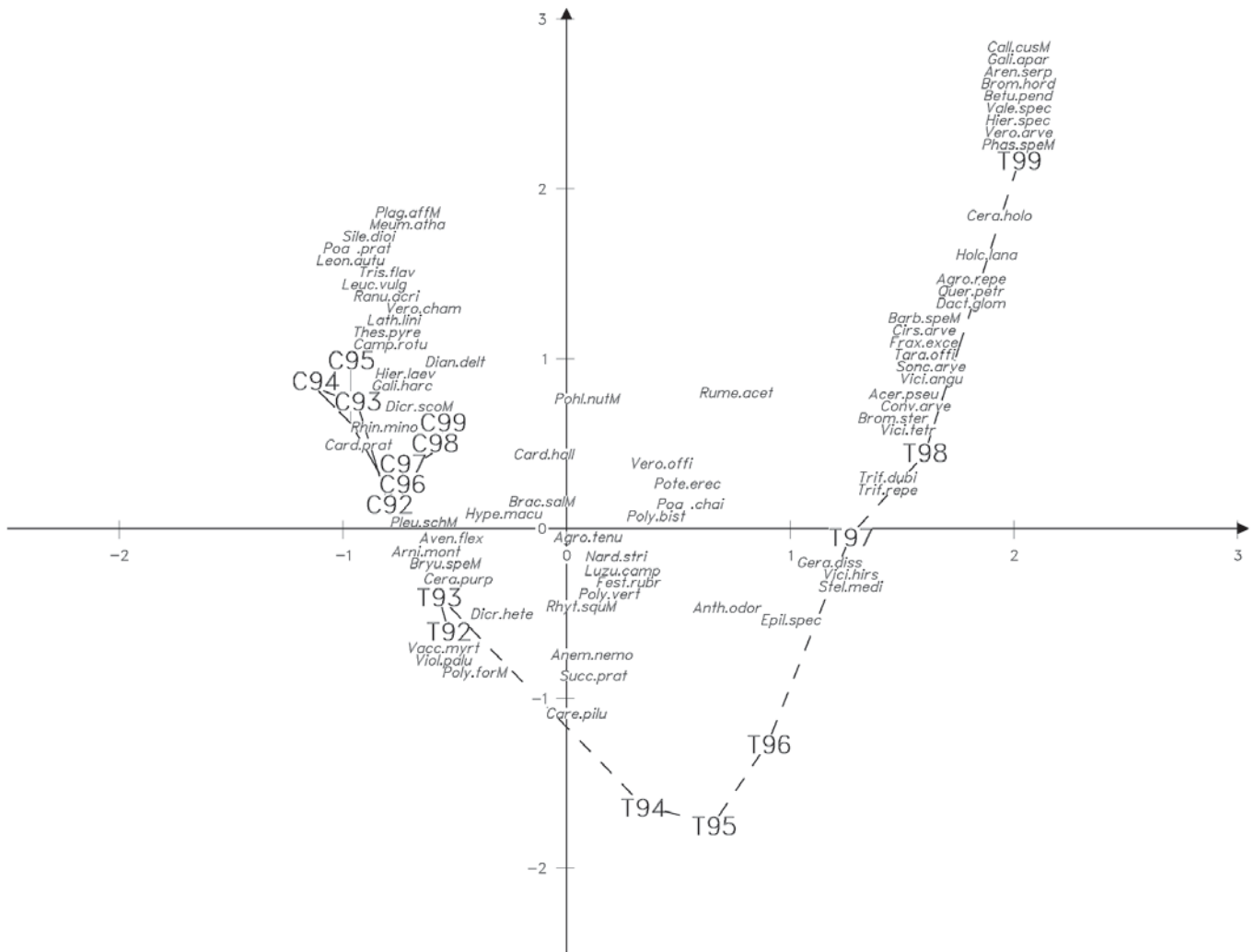


Fig. 2. Ordination diagram of 1st and 2nd CA axis. Bold letters refer to the plot translocated to 170 m (T) and the control plot at 600 m (C) with the two digit number giving the year of recording. Italics refer to species which are abbreviated by the first four letters of genus and epithets. Last letter M indicates a moss.

the dominant species (*Festuca rubra*, *Nardus stricta*, *Agrostis tenuis* and *Rhytiadelphus squarrosus*) in the last three years (Table 1).

The development of both plots with regard to each other is illustrated by the CA ordination (Fig. 2). In 1992, the two plots are only separated by a short distance which is mainly due to minor differences in cover of the dominant species and the lack of a few accompanying species in one of the plots. Since the translocation to 170 m reduced the cover of some species (e.g. *Agrostis tenuis*, *Luzula campestris*, *Hypericum maculatum*) to values of the initial state of the control plot at 600 m, the distance between T93 and C92 became even smaller in 1993 (Fig. 2). From then on, the plot at 170 m became progressively more dissimilar from that at 600 m with

the largest step from 1993 to 1994 when many species of group 5 were lost (Fig. 2; located on the left side) and from 1998 to 1999 when many new species established (Fig. 2; located on the right side). The species found in the centre of the diagram are common to both plots during the whole observation period. In comparison, the plot at 600 m experienced only a marginal change in position in the ordination diagram with the final state in 1999 being adjacent to the initial state in 1992.

Discussion

The response of the vegetation to the translocation to a lower altitude was species-specific. This was demonstrated by four montane species that had unreduced or increased growth (*Nardus stricta*, *Poa chaixii*, *Polygonatum verticillatum*, *Potentilla erecta*) in contrast to four other montane species that declined or died out (*Arnica montana*, *Meum athamanticum*, *Hypericum maculatum*, *Galium hircynicum*). The development of each species may be either a direct physiological response to the changed climatic conditions, or be indirectly caused by changed biotic interactions. The abiotic factors with a direct effect are available space, nutrients, temperature and humidity. Indirect effects may be caused by altered competition and herbivory levels. It is a common feature of manipulative field experiments at the community level that the factors mentioned above are interrelated and it is very difficult to distinguish between causes and effects (Chapin & Shaver 1985; Harte & Shaw 1995; Schappi 1996; Schappi & Korner 1996; Fischer et al. 1997). Nevertheless, an attempt will be made to discuss which species is influenced most by which factor.

Some of the factors mentioned are related to the disturbance caused by the translocation procedure. Since the disturbance was similar in both plots, it cannot be responsible for differences in species responses. However, some species obviously responded to the new available space in the gaps between sods. Bare soil was only present from 1993 to 1994, so the space effect could only have caused increased cover values in this period. The only species with an increase in this period and a subsequent decline was *Galium hircynicum* in the control plot.

Another disturbance effect generally caused by translocation is an enhanced nutrient supply. The nutrient effect was indirectly observed in both plots by increased height of the herb layer and increased litter production. The disruption of the soil structure and the consequent increased oxygen supply promote microbiological activity and increase mineralization. The process is comparable to the observed increase of the nitrogen mineralization rate when the soil structure is disturbed by filling soil into incubation bags (Gerlach 1973; Haynes 1986). The enhanced mineralization improves the nutrient supply of the plots and finally results in a higher biomass. This was observed in translocated litter meadows and mires (Klotzli 1975, 1978, 1987), chalk grasslands (Muller 1990) and in all meadow types in the Harz Mountains (Bruelheide & Flintrop 2000). In the control plot (600 m) the enhanced biomass production was mainly observed in the first two years following translocation; whereas it continued throughout the whole

observation period in the plot at 170 m. The biomass increase here may be, at least in part, due to the higher temperatures that promoted plant growth by accelerating physiological processes. However, in a field experiment heating a montane meadow in Colorado, Harte & Shaw (1995) found no significant increase in above-ground biomass in the treated plots. Apart from having direct effects on plant growth, higher temperatures have also probably increased mineralization rates (Haynes 1986). This interpretation is in agreement with the increase in cover of nitrogen demanding species such as *Rumex acetosa* and the establishment of species with high N_{iv} indicator values. In addition, species with a comparable low nutrient demand have also probably taken advantage of the increased nutrient supply, mainly those with a potentially high relative growth rate (RGR). Although the data on RGR given by Grime et al. (1988) refer only to seedlings under laboratory conditions, they may be also an indication for the growth rates of adults. The highest RGR of all matrix forming species in the plot is found for *Festuca rubra* and *Agrostis tenuis* ($1.0 - 1.4 \text{ wk}^{-1}$). This could indicate why *F. rubra* became dominant at 170 m. The observation that species of communities developed under harsh climatic conditions flourish when translocated to more moderate climates has been found in many studies, at least when competition was excluded (e.g. Dahl 1951; Gigon 1971; Volkova et al. 1999).

There is little evidence that species responded directly to the enhanced temperatures. On the one hand, most temperate plant species should be promoted by a temperature increase of the magnitude in the experiment (e.g. Woodward 1975, 1979; Grace 1988) and, on the other hand, most species are characterized by a remarkably high acclimatization ability (Billings & Mooney 1968; Friend & Woodward 1992). Among the species in this study, only *Meum athamanticum* appears to be an exception. The extinction of *M. athamanticum* as a matrix forming species gave rise to an eco-physiological study on the temperature response of this species (Bruelheide & Lieberum 2001). When *M. athamanticum* individuals of different ages were translocated to seven sites along an altitudinal gradient from 170 m to 1130 m a.s.l. in the Harz Mountains, the growth rates were found to differ only slightly, both between age stages and altitudes. Supplemental photosynthesis measurements on the acclimatization ability indicated that the species has a remarkably low phenotypical plasticity which probably does not allow to take advantage of the more favourable temperature conditions at lower altitudes. In addition, the loss of storage carbohydrates in *M. athamanticum* roots during the winter was much higher at lower altitudes (Bruelheide & Lieberum 2001). A high carbon loss in winter would

explain the less vigorous growth observed for *M. athamanticum* in the year following translocation. Since species from high altitudes are generally characterized by high respiration rates (Mooney & Billings 1961, 1965; Billings 1974; Stewart & Bannister 1973, 1974), the loss of storage carbohydrates may also play a role in the other declining species.

Another site factor to be considered is the changed soil and air moisture at 170 m, which might have caused the decline and extinction of species requiring high moisture levels such as *Succisa pratensis* and *Viola palustris*. However, the constant cover of the third and most abundant moisture demanding species, *Polygonum bistorta*, shows that low humidity was probably not the limiting factor for montane species.

The decline of most species in the plot at 170 m is probably not due to direct climatic effects but caused indirectly by an increased level of competition for light, caused by the increase in above-ground biomass. This hypothesis is supported by the fact that most declining species had a low stature, such as *Galium hircynicum*, *Arnica montana*, *Campanula rotundifolia*, *Veronica chamaedrys* and all mosses of mat-grass swards. Such effects are also known from open-top chamber experiments with elevated CO₂ levels. For example, Fischer et al. (1997) found the reduced survival of the low growing *Gentianella germanica* to be caused by increased competition mediated by increased total above-ground biomass. However, this interpretation does not explain the fact that not all low-growing species declined in cover (e.g. *Luzula campestris*, *Rhynchospora squarrosus*) and that there was still a considerable amount of open space even late in the investigation period, mainly created by mice which allowed the establishment of the species of group 6 (Table 1).

There is another possible explanation for the extinction of *Arnica montana* other than competition for light. In food choice experiments *A. montana* was found to be extremely palatable for different slug species (Scheidel & Bruelheide 1999). This led to the hypothesis that the geographical range of *A. montana* is limited by slug herbivory. In a translocation experiment to sites of different altitudes the damage was negligible at 610 m; whereas most *Arnica* individuals were eaten at 180 m (Bruelheide & Scheidel 1999). By protecting the translocated plants with polyethylene nets and thus reducing the level of slug herbivory, the damage at lower altitude was reduced significantly. Conversely, the increase in herbivory pressure by releasing slugs into native *A. montana* populations at 600 m resulted in significantly increased damages (Bruelheide & Scheidel 1999). These observations explain why no translocated *A. montana* individuals survived for more than one year in this study. Among the declining species a high

palatability for slugs is only known for *A. montana* but it cannot be ruled out that other montane species are also considerably affected by slug herbivory. For example, Scheidel & Bruelheide (2001) found a significantly higher palatability of the montane *Senecio hircynicus* compared to the widespread *S. ovatus*. Apart from damaging plant tissues biotic interactions are also known to have a crucial impact on reproduction. For *Hypericum perforatum*, a species that is morphologically very similar to *H. maculatum*, Fox et al. (1999) demonstrated, in a manipulative field experiment, that reduced summer precipitation increased the vulnerability of the plants to insect herbivory on flowers and capsules.

At the community level, the observed individual species responses when translocated to lower altitude have remarkable consequences. Species that grow together at 600 m are no longer found growing together at 170 m. Although the similarity to the initial state is still 45% and the occurrence of *Nardus stricta* still allows the stand to be termed a mat-grass community, the floristic composition has changed considerably. When the community is defined by the presence of differential species, as is common practice in Central European vegetation classification, the stand can no longer be assigned to the *Polygalo-Nardetum* (Peppler 1992; Bruelheide 1995). It is still too early to predict whether the remaining montane species will persist. If they do, a new type of mat-grass community would be the result. In this respect, the experiment supports the hypothesis that global climate change might give rise to new communities. This view is also supported by field experiments on plant communities that involved manipulative increases of air or soil temperature (Chapin & Shaver 1985; Harte & Shaw 1995). The individual species response resulted in changed dominances of species and changed floristic compositions.

The same opinion is held by palaeobotanists who have found species-specific responses in the rate and the direction of plant species migration in the Quarternary (Huntley & Webb 1989). Isopoll maps show that species sharing a similar geographical distribution today were not found together in many parts of Europe and North America 6000 B.P. when the summer climate was thought to have been warmer with more pronounced seasonality. Huntley (1991) concludes from this that communities are merely temporary assemblages of species that dissociate and re-associate in different assemblages as climate changes. Evidence for this hypothesis is also found in microcosm experiments (Davis et al. 1998). In incubator boxes *Drosophila subobscura* had an optimum temperature of 15 °C when kept without competition and at 10 °C when kept together with two other *Drosophila* species and a parasitoid wasp (*Leptopilina boulardi*) (Davis et al. 1998).

The outcome of the experiment presented here emphasizes the importance of considering biotic interactions when predicting the impacts of climate change. The change in altitude involved not only changes in climatic conditions but also changes in the whole constellation of site factors. This questions correlative approaches that are based on single species. Even when based on ecophysiological experiments, the kind of challenge that a species will be confronted with is not predictable from the response of a single species. However, the encountered complexity of factors in the translocation experiment is still much smaller than can be expected to be seen in nature with a future climate change.

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