

# Potential effects of climate change on plant species in the Faroe Islands

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## ABSTRACT

**Aim** To identify the effect of climate change on selected plant species representative of the main vegetation types in the Faroe Islands. Due to a possible weakening of the North Atlantic Current, it is difficult to predict whether the climate in the Faroe Islands will be warmer or colder as a result of global warming. Therefore, two scenarios are proposed. The first scenario assumes an increase in summer and winter temperature of 2 °C, and the second a decrease in summer and winter temperature of 2 °C.

**Location** Temperate, low alpine and alpine areas in the northern and central part of the Faroe Islands.

**Methods** The responses of 12 different plant species in the Faroe Islands were tested against measured soil temperature, expressed as  $T_{min}$ ,  $T_{max}$ , snow cover and growing degree days (GDD), using generalised linear modelling (GLM).

**Results** The tolerance to changes in winter soil temperature (0.3-0.8 °C) was found to be lower than the tolerance to changing summer soil temperature (0.7-1.0 °C), and in both cases lower than the predicted climate changes.

**Conclusions** The species most affected by a warming scenario are those that are found with a limited distribution restricted to the uppermost parts of the mountains, especially *Salix herbacea*, *Racomitrium fasciculare*, and *Bistorta vivipara*. For other species, the effect will mainly be a general upward migration. The most vulnerable species are those with a low tolerance, especially *Calluna vulgaris*, and also *Empetrum nigrum*, and *Nardus stricta*.

If the climate in the Faroe Islands should become colder, the most vulnerable species are those at low altitudes. A significantly lower temperature would be expected to produce a serious reduction in the extent of *Vaccinium myrtillus* and *Galium saxatilis*. Species like *Empetrum nigrum*, *Nardus stricta*, and *Calluna vulgaris* may also be vulnerable. In any case, these species can be expected to migrate downwards.

#### **Keywords**

Alpine species, climate change modelling, cold summer, Faroe Islands, North Atlantic Current, oceanicity, soil temperature, vegetation change, warm winter.

#### INTRODUCTION

General circulation models (GCM) of the earth's climate system are predicting that the continued increase of atmospheric  $CO_2$ will cause rapid warming of the earth during this century (IPCC, 2001). The discussion of possible effects of climate change on vegetation has tended to focus on continental areas or on the global scale, where zones of extensive homogeneous vegetation or ward, 1987, 1992; Prentice *et al.*, 1992; Sykes *et al.*, 1996; Ni *et al.*, 2000). Vegetation changes in oceanic and coastal areas have in general had little attention compared to continental areas. Because of a relatively small temperature range during the year, oceanic and coastal areas are different from continental areas and may respond differently, thus requiring individual consideration (Crawford, 2000, 2001). In particular, the North Atlantic oceanic

biomes are found in relatively similar climatic regions (Wood-

areas have been little studied in this regard, but according to predictions, global warming in oceanic areas in NW Europe will be accompanied by increased cloudiness and precipitation (IPCC, 2001).

The Faroe Islands are situated in the North Atlantic Current, where potential vegetation changes in a climate change scenario will occur under oceanic conditions that are difficult to predict, due to the large uncertainty in future climate development in this region (IPCC, 2001). The region around the Faroe Islands is considerably warmer than other areas at similar latitudes (Rahmstorf, 2002) due to the enhanced heating effect from the North Atlantic Current (Hansen & Østerhus, 2000). Climate changes in the 21st century, as predicted by some climate models, indicate the possibility of a weakening of the North Atlantic Current, which is supported by some observations (Hansen *et al.*, 2001). If such a weakening were to occur, temperatures in the Faroe Islands may decrease rather than increase. Assessments of future vegetation changes in the Faroes must therefore take into account both a warming and a cooling scenario.

In oceanic areas, the difference between the summer and winter temperatures is small. It is generally assumed that the most critical conditions for the vegetation in oceanic areas are: (1) the low summer temperature, which prevents plants from bearing fruit; and (2) mild winter periods, which disturb the inactive period (Crawford, 2000), causing the plant to start growth too early, and subsequently to be damaged by frost.

The lower limit of  $T_{max}$  (average temperature in August) required for a plant species represents the minimum temperature requirement during the growing season, which is also a rough measure of available solar energy. The upper limit of  $T_{max}$  serves to estimate the point where metabolic collapse may occur. This is especially important for plants adapted to a cooler environment (Box, 1981). The lower limit for  $T_{min}$  (average temperature in February) specifies the minimum temperature that can be tolerated by a species, while the upper limit represents the low temperature that induces dormancy in seasonal plants (Box, 1981) and which has been used to describe the southern limits of some species (e.g. Sykes *et al.*, 1996; Dahl, 1998).

The distribution of mountain plants may be seriously affected by climate change (Huntley, 1991; Körner, 1995; Crawford, 1997). The effects of warming can be categorised as: (1) upward migration of plant species; and (2) disappearance of snow patches and their associated communities (Grabherr *et al.*, 1995). Both can lead to the disappearance of species if the mountains are not high enough to allow the species to migrate to a higher altitude (Grabherr *et al.*, 1995). In continental areas, however, only a few examples have been found of species that are likely to become extinct on mountain summits within the next century (Körner, 1995, 1998). While the effects of cooling have received only little attention, they are nevertheless likely to lead to a downward migration and even the possible retreat southwards of lowland species.

The effect of climate change in oceanic mountains is buffered by the ocean due to the limited annual temperature range (Crawford, 2000). However, the relative scarcity of species on mountains in oceanic areas of south-western Norway and the Scottish Highland is considered partly to be due to the effect of mild winter temperatures (Dahl, 1990; Crawford, 2001). In Norway, these species, absent from mountainous areas, are described as southwest coast avoiders (Dahl, 1951, 1990).

It is generally accepted that species respond in an individualistic manner to climate in both space and time (Gleasson, 1926; Chapin, 1985). The potential impact of climate change has been studied at the individual species level (Chapin & Shaver, 1985; Crawford, 1997; Sætersdal & Birks, 1997) and on a broader scale in plant communities or vegetation zones (Woodward, 1983; Peters & Darling, 1985; Molau & Alatalo, 1998; Duckworth *et al.*, 2000). Although the species respond as individuals, studies at the vegetation level are necessary to put species into a broader context.

In this paper, 12 indicator species of the vegetation in the Faroe Islands (Fosaa, in press) are tested against different temperature parameters based on the vegetation from five mountains. The main aim is to estimate the response values (optima and tolerance) of the species in relation to February and August mean temperature, GDD, and snow cover. From these responses, we identify which of the species are likely to be affected by changes in summer temperature and winter temperature. Due to the uncertainty of changing climate in the Faroes, the vegetation changes are discussed both in relation to a warming and a cooling scenario.

# STUDY AREA

The Faroe Islands is a treeless archipelago situated on the border between the arctic and temperate environment, between 61°20' and 62°24' N and between 6°15' and 7°41' W (Fig. 1). The climate in the Faroe Islands is strongly influenced by the warm North Atlantic Current and by the proximity to the low-pressure track in the North Atlantic region. Consequently, the climate is humid, variable, and windy. The warmest months in the Faroe Islands are July and August, with a mean temperature of 11 °C (lowland), and the coldest is February, with a mean of 4 °C (lowland). The mean precipitation in the Faroe Islands is 1500 mm annually (lowland). The precipitation reflects the topography of the islands, such that the coastal areas receive around 1000 mm per year, increasing to more than 3000 mm in the central parts (Cappelen & Laursen, 1998). The nearest neighbour, the Shetland Islands, is 345 km to the south-east. The Faroe Islands consists of 18 islands separated by narrow fjords with a total land area of 1400 km<sup>2</sup> and a distance from north to south of 113 km and from east to west of 75 km. The highest mountain peak is 882 m above sea level (a.s.l.)

The predominant vegetation in the Faroe Islands is grassland, occurring from sea level to the mountain top. Three vegetation zones have been defined in the area. One lowland vegetation zone (below 200 m a.s.l.) with moist dwarf shrub heath as the main vegetation type. Dominant species in this zone are *Calluna vulgaris* and *Empetrum nigrum*. This vegetation type is replaced by moist grassland vegetation, which represents the low arctic alpine zone up to 400 m a.s.l., while *Racomitrium* and open grassland vegetation represent the alpine vegetation zone (Fosaa, in press). The soil is relatively poor in nutrients (Lawesson *et al.*, 2003). The pH increases from the lowlands to the mineral soil in the highlands (Olsen & Fosaa, 2002).



**Figure 1** Location of the Faroe Islands and location of the five studied mountains in the Faroe Islands: 1: Sornfelli; 2: Mosarøkur; 3: Ørvisfelli; 4: Gráfelli and 5: Villingardalsfjall.

#### MATERIALS AND METHODS

## Vegetation and soils

In July–August 1999 and 2000, the vegetation on five mountains in the Faroe Islands was sampled along five transects, from the top (856 m a.s.l.) down to 150–100 m a.s.l. (Fig. 1). The vegetation

 
 Table 1 Indicator species for the vegetation in the three different vegetation zones
 was sampled in 50-m altitudinal intervals within 100 m<sup>2</sup> quadrats (macro-plots). In each macro-plot, 8 smaller ( $0.25 \text{ m}^2$ ) quadrats (meso-plots) were placed randomly. The meso-plots were subdivided into 25 ( $0.01 \text{ m}^2$ ) microplots and the presence/absence of each plant species was noted for each microplot. In this way, the abundance of species, ranging from 1 to 25, was determined for each meso-plot.

The vegetation was classified into three significant altitudinal groups, including 12 plant communities (Fosaa, in press). The species that were used to define the plant communities were species with high abundance and high constancy in the communities. These 12 species were used as indicator species for the vegetation in the area (Table 1) and were used to test the effect of changing climate in this study.

#### Soil temperature

Hourly soil temperatures were measured 1 cm below the soil surface at 50-m altitudinal intervals on the five mountains using TinyTags data loggers. The period of measurement was from September 1999 to August 2000 for all the mountains except for Mosarøkur (M), where the period was August 2000 to July 2001. Details of the measurements and their processing have been reported by Fosaa et al. (2002). To extract characteristic features, values for five key parameters were computed: the annual mean temperature  $(T_{mean})$ ; the mean temperature in August  $(T_{max})$ ; the mean temperature in February (T<sub>min</sub>); growing degree days (GDD); and number of days with snow cover. GDD was calculated by summing the temperature excess over 5 °C for all hourly observations in a year and dividing by 24 (Molau & Mølgaard, 1996). Number of days with snow cover was calculated as the number of days with daily temperature range below 0.5 °C and the average daily temperature below 1 °C.

#### Data analysis

A total of 237 sample plots from 5 mountains (Fig. 1) were included in the analyses. The relationships between the 12 indicator species and the climate parameters were first tested with a CCA analysis (Canonical Correspondence Analysis). The computer program CANOCO was used for all the statistical analyses (ter Braak & Smilauer, 2002).

The distributions of the 12 indicator species were then tested against  $T_{min}$ ,  $T_{max}$ , snow cover, and growing degree days (GDD) using generalized linear modelling (GLM) in order to find the

Alpine vegetation zone	Low alpine vegetation zone	Temperate vegetation zone
Salix herbacea L.	Nardus stricta L.	Calluna vulgaris L. (Hull.)
Bistorta vivipara (L.) S. F. Gray	Galium saxatilis L.	Empetrum nigrum L.
Koenigia islandica L.	Vaccinium myrtillus L.	
Racomitrium lanuginosum (Hedw.) Brid.		
Racomitrium fasciculare (Hedw.) Brid.		
Festuca vivipara (L.) Sm.		
Deschampsia flexuosa (L.) Trin.		

optimum and the tolerance of each species. The GLM model is a regression model sharing the same basic properties of the response variables and the predictors as traditional linear models. In the GLM model, the expected values of the response variables are not supposed to be always directly equal to the linear combination of the predictor value (ter Braak & Smilauer, 2002).

A GLM analysis was performed for each of the four climate parameters against the 12 indicator species. The abundance of the species was used as the response variable and climate parameters were used as predictor variables. Since responses are discrete values (count of presence/absence in microplots), a Poisson error distribution and a logarithmic link were assumed (McCullagh & Nelder, 1989). In order to find the best model, the GLM was tested using zeroth, first and second-order polynomials, with a forward selection at a significance level of 0.05. An F-test was used to evaluate the statistical significance of the model. In general terms, this means that species abundance dependencies on the climate variables were fitted to either a constant (zeroth order), an exponential (first order), or a Gaussian (second order) function, using least squares regression. This procedure does not allow for unimodal response curves that are skewed. Using the methodology of Huisman et al. (1993), it was found that some species would have been better described by skewed response curves, but optima and tolerances were not found to be substantially altered by this procedure.

The species most vulnerable to climate change are those with narrow tolerances. With increasing temperatures, species with low optima will also be vulnerable, while species with high optima will be vulnerable to decreasing temperatures.

## RESULTS

The distribution of the 12 indicator species is shown in Fig. 2. The indicator species for the temperate and low alpine zone (Table 1) are seen to have their main distribution below 400 m a.s.l. *Calluna vulgaris* has the lowest distribution, almost disappearing at 300 m a. s.l. *Galium saxatilis* and *Deschampsia flexuosa* have higher altitude distribution areas, up to 600 and 700 m a.s.l., respectively. Most of the species defined as indicators for the alpine vegetation zone have their main distribution area above 300–400 m a.s.l. *Festuca vivipara* and *Racomitrium lanuginosum* are exceptions, as they are almost as abundant in the temperate and low alpine zone as in the alpine zone.

Results from the soil temperature measurements for two opposing aspects are shown in Fig. 3a–e. Most of the temperature parameters are significantly higher (P < 0.05) on the southfacing transect than on the north-facing transect except for  $T_{min}$ , which was the same at the top of the two mountains, and snow cover, which is higher on the north-facing slope along the whole transect.

Results from the CCA show that the eigenvalues of axis 1 and 2 were 0.587 and 0.11, respectively (Fig. 4). The speciesenvironmental correlation for axis 1 was 0.917 and for axis 2 was 0.517. The variance in species data accounted for by the first axis was 17.3% and for the second axis was 3.3%. The Monte Carlo permutation test showed that these values were significant at P < 0.01. The four climate parameters studied are not independent of one another. In the CCA analysis (Fig. 4)  $T_{\rm ave}$  is described best by axis 1 with GDD second, and then finally  $T_{\rm min}$ . While  $T_{\rm min}$  is not the parameter best described by axis 1, the discussion will focus on  $T_{\rm min}$  and  $T_{\rm max}$  because they capture the distinctive character of axis 1 and axis 2, respectively. The following discussion therefore focuses on these two parameters, and attempts to evaluate vegetation changes in each of the two scenarios.

 $T_{min}$ ,  $T_{max}$ , and GDD were negatively correlated with snow cover. The indicator species split into two, with species from the alpine zone (*Festuca vivipara*, *Deschampsia flexuosa*, *Koenigia islandica*, *Racomitrium lanuginosum*, *R. fasciculare*, *Salix herbacea* and *Bistorta vivipara*) in one grouping, and species from the low alpine and temperate vegetation zones (*Calluna vulgaris*, *Empetrum nigrum*, Vaccinium myrtillus, *Nardus stricta* and *Galium saxatilis*) in the other. Alpine species scores were positively correlated with snow cover, and therefore negatively correlated with high temperatures, while low alpine and temperate species scores were positively correlated with high temperatures, and therefore negatively correlated with high temperatures, and therefore negatively correlated with snow cover.

The results from the GLM analysis are shown in Table 2 and Fig. 5a–d for four different climate parameters. For the species with unimodal response curves, the optimum indicates the parameter value for which maximum abundance occurs, while the tolerance is a measure of the width of the curve, defined as the amount of parameter deviation from the optimum needed to decrease the abundance to  $e^{-0.5}$  (61%) of the maximum.

For  $(T_{min}, T_{max})$ , the GLM analysis gave significant estimates for most of the species. Only three species showed optima and tolerance for August temperature, and these three species were indicator species for the temperate and low alpine zone. The optimum varied from 12.1 °C to 13.0 °C and the tolerance from 0.7 °C to 1.0 °C. The alpine species were found to have their optima below the range of the observed temperature.

Optimum February temperatures were found to vary from -1.1 °C to 1.3 °C and the tolerances from 0.8 °C and 0.3 °C, respectively. For snow cover, the optima varied from 46 to 141 days and the tolerances from 20 to 54 days. For GDD, the optima varied from 547 to1155 and tolerances from 134 to 202 (Table 2 and Fig. 5a–d).

#### DISCUSSION

Mountain ecosystems are complex units influenced by a range of different environmental factors. It is the sum of the changes of these factors operating together that determines the distribution of the vegetation. Many facets of the microclimate of plants change with altitude (Geiger *et al.*, 1965) and some of these changes control the pattern of the distribution of plant species (Woodward, 1983).

In this study, the altitudinal distribution of 12 indicator species in the Faroe Islands have been investigated and related to temperature. The species studied have their main distribution areas either south or north of the Faroes. The species from the temperate vegetation zone (*Calluna vulgaris* and *Empetrum nigrum*) have their distribution area mainly south of the Faroe



Figure 2 Scatterplot of the distribution of the 12 indicator species on the five investigated mountains. The analysis was based on 237 meso-plots  $(0.25 \text{ m}^2)$  from five mountains in the Faroe Islands. The value on the *Y*-axis is the abundance of species from 1 to 25. m a.s.l. = metres above sea level.



**Figure 3** a–e Regression lines for five different temperature parameters on two opposing mountain slopes: N is a north-facing slope and S is a south-facing slope. Lr = Lapse rate. (a) T <sub>ave</sub> (°C) (b) T<sub>max</sub> (°C) (c) T<sub>min</sub> (°C) (d) GDD and (e) snow cover. The north-facing slope are the mountains 1: Sornfelli and 3: Ørvisfelli The mountains from the south-facing slope are 2: Mosarøkur, 4: Gráfelli and 5: Villingardalsfjall. See Figure 1 for further details. The temperature was measured from the period September 1999 to August 2000 for all the mountains except Mosarøkur where the period was August 2000 to July 2001.

Islands (Hultén & Fries, 1986) and the species from the low alpine and alpine vegetation zones (Table 1) are mainly distributed in the arctic area (Hultén & Fries, 1986).

Global warming in oceanic areas in north-western Europe under conditions of doubling of atmospheric CO<sub>2</sub> (IPCC, 2001) is expected to be accompanied by elevated precipitation and cloudiness, and perhaps also increased wind speed (Furevik et al., 2002). This will, of course, make the prediction of species response to increasing or decreasing temperature more complicated. Calluna vulgaris is a species that dominates the heathland communities in the Faroe Islands. This species is restricted to south-facing slopes, since it needs both sun and warmth. Therefore, this species would most likely be vulnerable to increased cloudiness under both warming and cooling conditions (Heide-Jørgensen & Johnsen, 1997). Increased wind speeds would also be expected to affect the vegetation. Lowland species have been shown to be more sensitive to high wind speed than highland species (Woodward, 1983, 1993; Beerling & Woodward, 1994). Heavy rainfall causes the soil profile to be water-saturated for extended periods, especially during winter and spring (Crawford, 1997) and extensive root dieback has been found in plant species growing in a water-saturated soil profile (Crawford, 2000). Many plant species respond to elevated atmospheric CO<sub>2</sub> by a higher rate of photosynthesis and partial closure of stomata. These responses increase water-use efficiency, especially in drought prone areas. Some species are also stimulated to grow faster under elevated atmospheric CO<sub>2</sub> (e.g. Körner, 1999) while others may reduce their competitive ability (Theurillat & Guisan, 2001), leading to structural changes in the vegetation.

Considering only the effects of changing temperatures on the vegetation is therefore an oversimplification. For the Faroese vegetation, we have, however, little quantitative information on the effects of these various climate parameters on the vegetation and focus therefore on temperature only.

In our study, we have only investigated the effects of soil temperatures, while climate scenarios involve air temperature. To what extent changes in these two parameters will be equal is not clear, especially for temperatures close to freezing, but generally one would expect them to change in the same direction. This is reflected in Fig. 3, where the lapse rate for average and maximum soil temperature is somewhat smaller, but still of the same order of magnitude as the lapse rate of the air temperature (0.8 °C per 100 m, according to Christiansen & Mortensen, 2002). In any case, the magnitude of future temperature changes can only be forecast with large uncertainties and we do not therefore distinguish between air and soil temperatures in the discussion.

We have only used temperature measurements for a relatively short period (1999–2000), when compared to the time needed for vegetation to reach equilibrium (Grabherr *et al.*, 1995). This was because there were no long time series of temperatures at many altitudes in the Faroe Islands. Long-term air temperature observations in Tórshavn indicate, however, that the 1999–2000 period was fairly normal when seen in a longer term climate perspective (Cappelen, 2003).

The tolerance to changes in winter temperature in our study (0.3-0.8 °C) is lower than the tolerance to changing summer

Figure 4 Canonical Correspondence Analysis showing the relationship between the 12 indicator species and climate parameters. The indicator species are selected on the basis of those species with highest abundance and constancy in the plant communities. The eigenvalues for axes 1 and 2 were 0.587 and 0.111, respectively. The species-environmental correlation for axis 1 was 0.917 and for axis 2 was 0.517. The variance in species data was 17.3% for axis 1 and 3.3% for axis 2. The Monte Carlo permutation test showed that these values were significant at P < 0.01. The analysis was based on 237 meso-plots (0.25 m<sup>2</sup>) from five mountains. See text for full species names.



**Table 2** Optimum and tolerance of summer and winter temperature, growing degree days (GDD) and snow cover for 12 species from five mountains in the Faroe Islands. The optimum indicates the parameter value for which maximum abundance occurs, while the tolerance is a measure of the width of the curve. Peak is the maximum abundance, on a scale from 0 to 25, being the range of possible scores within each of the 237 meso-plot ( $0.25 \text{ m}^2$ ) and *P* is the significance of the model. Based on 237 meso-plots from five mountains. See text for full species names

Species	Р	Optimum	Tolerance	Peak	Р	Optimum	Tolerance	Peak
T <sub>max</sub> (°C)					T <sub>min</sub> (°C)			
Call vul	$< 1.0 \times 10^{-6}$	12.4	0.7	5.3	$< 1.0 \times 10^{-6}$	1.1	0.3	16.0
Emp her	$< 1.0 \times 10^{-6}$	13.00	1.0	4.3	$< 1.0 \times 10^{-6}$	1.0	0.3	7.8
Vac myr	$< 1.0 \times 10^{-6}$	> 14.00		_	$< 1.0 \times 10^{-6}$	0.9	0.4	2.3
Gal sax	0.0003	> 14.00		_	0.01	0.3	0.3	3.7
Nar str	$< 1.0 \times 10^{-6}$	12.1	1.0	5.0	$< 1.0 \times 10^{-6}$	1.3	0.6	11.1
Des fle	0.002	< 6		_	0.00009	-0.3	0.3	1.9
Fes viv	0.4	_	_	_	0.0001	-0.1	0.8	4.0
Koe isl	_	_	_	_	0.0002	-0.4	0.4	2.3
Rac fas	0.000003	< 6	_	_	$< 1.0 \times 10^{-6}$	< -2		
Rac lan	0.003	> 14	_	_	0.007	> 2	_	_
Sal her	$< 1.0 \times 10^{-6}$	< 6	_	_	$< 1.0 \times 10^{-6}$	-1.1	0.6	10.7
Bis viv	0.00001	< 6	—	—	$< 1.0 \times 10^{-6}$	-0.9	0.7	6.8
GDD					Snow cover (days)			
Call vul	0.006879	1128	145	8.0	0.00017	47	20	7.2
Emp her	$< 1.0 \times 10^{-6}$	1155	151	6.5	$< 1.0 \times 10^{-6}$	59	29	4.1
Vac myr	$< 1.0 \times 10^{-6}$	> 1200	_	_	0.00003	69	33	1.4
Gal sax	0.02	> 1200		_	_	_	_	_
Nar str	$< 1.0 \times 10^{-6}$	1062	202	6.4	$< 1.0 \times 10^{-6}$	< 50	_	_
Des fle	$< 1.0 \times 10^{-6}$	< 200		_	$< 1.0 \times 10^{-6}$	> 150	_	_
Fes viv	0.01	_		_	0.01	141	54	4.2
Koe isl	0.001	666	146	1.7	0.02	121	38	1.5
Rac fas	0.03	547	134	3.7	0.0001	130	41	2.8
Rac lan	0.00004	< 300	_	_	0.003	< 50	_	_
Sal her	0.06	< 300		—	$< 1.0 \times 10^{-6}$	> 150	_	_
Bis viv	0.08	571	180	5.5	$< 1.0 \times 10^{-6}$	> 150	—	—

temperature (0.7–1.0 °C). Comparing these results with tolerance of mountain plant species in Norway (Sætersdal & Birks, 1997) we found that the tolerance for changing winter temperature in our study is 10 times lower, but the summer temperature tolerances were at the same level. This may indicate that warm winters in oceanic areas like the Faroe Islands may be most critical for plant species during a climate warming regime. But here it is also important to take into consideration that the measured temperature in our study is soil temperature, and the constant freezing and thawing activity in the islands (Humlum & Christiansen, 1998; Christiansen & Mortensen, 2002) affects our result to some degree.

As noted in the introduction, the potential temperature change in the Faroe Islands is more uncertain than for most



Figure 5 a–d Results of the GLM analysis for the 12 indicator species and climate parameters (a) mean soil temperature in August  $(T_{max})$  (b) mean soil temperature in February  $(T_{min})$  (c) growing degree days (GDD) (d) snow cover. For the species with unimodal response curves, the optimum indicates the parameter value for which maximum abundance occurs, while the tolerance is a measure of the width of the curve. See text for further details and full species names.

other regions. According to some models, the Faroese climate will warm on the order of 2 °C in the 21st century (Furevik *et al.*, 2002). If, on the other hand, the North Atlantic Current flow past the Faroes were to weaken significantly, the associated decrease in oceanic heat transport might lead to a net cooling of the same order of magnitude.

It has therefore been necessary to examine two different scenarios, one with warming, and the other with cooling. It is generally assumed that winter temperatures will change more than summer temperatures (IPCC, 2001). How applicable this is to an extreme oceanic climate like in the Faroe Islands is, however, doubtful. For simplicity therefore the same change, on the order of 2 °C, for both the summer and winter temperature in both scenarios has been assumed herein.

Assuming that the temperature in the Faroe Islands would change according to either of these scenarios, the simplest change to be expected, would be an up- or downward migration of the vegetation zones. With a lapse rate of 0.8 °C per 100 m (Christiansen & Mortensen, 2002), a change in the air temperature by 2 °C, would be equivalent to a vertical movement on the order of 250 m. This, of course, may not be possible in a warming scenario for plants already located on the mountain tops, or in a cooling scenario for plants whose present distribution is at sea level.

While the effects of cooling have received only little attention, they are nevertheless likely to lead to a downward migration and even the possible retreat southwards of lowland species. There is some evidence for downward migration of vegetation zones during the last century due to cooling in the Faroe Islands. The climate in the Faroe Island was about 0.25 °C warmer in the late 1930s than in the last decade of this century. Comparing vegetation zones from vegetation studies in the late 1930s (Böcher, 1937) and vegetation studies in 1999–2000 (Fosaa, 2003) the vegetation zones were found at a considerably lower altitude in the latter period.

Although climate change might lead to migration of species, a time lag between the change in climate and the migration might be expected (Grabherr *et al.*, 1995). Therefore, the change in distribution of plant species would not be expected to be at the same magnitude as the climate change in this century. In addition, plant species in alpine environments have the ability to persist as an adult individual for a considerable time (Crawford, 1989). Further, these species might have enough genotypic variability to allow them to adapt to the changing climate. However, evidence from past climate change indicates that species respond by migration rather than by adapting genetically (Huntley, 1991).

## CONCLUSIONS

Scenario I. In this scenario, both  $T_{min}$  and  $T_{max}$  are assumed to increase by about 2 °C. The warming scenario will result in upward migration of plant species as a result of elevated temperature. The species most vulnerable to elevated summer temperature are those species currently restricted to the uppermost parts of the mountains: especially *Salix herbacea, Racomitrium fasciculare,* and *Bistorta vivipara* (Fig. 5a).

As species respond in an individual way to changing climate (Chapin & Shaver, 1985) and migrate at different rates (Grabherr *et al.*, 1995), plant species as well as plant communities in the alpine zone are threatened by competitive species from lower altitudes. The total vegetation cover in the alpine zone is much lower than in the low alpine and temperate zones below (Fosaa, in press). Thus, the alpine zone should be more easily invaded due to higher frequency of bare soils in these areas and less competition from other species, although the environment is much harsher.

Elevated summer temperature will tend to allow the upward migration of temperate and low alpine species. The most vulnerable species are those with a low tolerance (Fig. 5a), especially *Calluna vulgaris*, but also *Empetrum nigrum*, and *Nardus stricta*. From Fig. 5(a), one would also expect *Vaccinium myrtillus* and *Galium saxatilis* to extend their distribution upwards, but from the analysis, we cannot establish how sensitive they are.

Mild winters can be a threat to plants by disturbing their inactive period and can cause loss of frost hardiness (Ögren, 1996). As seen from the GLM analysis (Fig. 5a and b), the tolerances for  $T_{min}$  are considerably smaller than those for  $T_{max}$ , and, for most of the species, are well below the assumed temperature increase of 2 °C. As indicated previously, the low tolerance of most species to

changing winter temperature is the striking difference between tolerance of species in oceanic environments like the Faroe Islands and the tolerance of mountain plants in more continental areas (Sæterdal & Birks, 1997). Generally, increasing  $T_{min}$  tends to affect the individual species in the same manner as increasing  $T_{max}$  (Fig. 5a,b).

Scenario II. In this scenario, we assume a temperature decrease of about 2 °C. The species most vulnerable to decreasing temperatures are those restricted to low altitudes. A lower summer temperature would be expected to produce a serious reduction in the extent of *Vaccinium myrtillus* and *Galium saxatilis*. Species like *Empetrum nigrum*, *Nardus stricta*, and *Calluna vulgaris* may also be vulnerable. In any case, these species can be expected to migrate downwards (Fig. 5a).

In contrast to the first scenario, lower winter temperatures are generally expected to affect plant species positively, since lower winter temperatures reduce disturbance of plants during winter dormancy (Crawford, 2000). A lowering of the temperature by 2-3 °C would most likely be enough to establish meteorological conditions for widespread discontinuous permafrost in the high mountains (Humlum & Christiansen, 1998). These changing environmental conditions will presumably alter the conditions for the alpine plants species on the mountain top, and the distribution area for the alpine plant species would also shift downward.

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