Chapter 1: Introduction

1.1. Background: Evidence for climatic shifts in mountain vegetation

The global climate has shown an increase of 0.6°C over the last century and is predicted to rise between 1.5°C and 5.8°C over the next century (IPCC 2001). Ecosystems at high altitudes and latitudes are expected to be particularly sensitive to climatic change (Pauli *et al.* 1996). A number of models, using a climate envelope approach, has predicted reductions in species distribution for arctic/alpine plants due to climate change (e.g. Huntley *et al*. 1995, Cannell *et al*. 1997, Harrison *et al*. 2001, Bakkenes *et al*. 2002, Berry *et al*. 2002, Pearson *et al*. 2002, Thomas *et al*. 2004), due to loss of suitable climatic conditions. For example, over recent years there has been increasing evidence that plant species in mountain areas are being found at higher altitudes than previously (Grabherr *et al.* 1994, Keller *et al.* 2000, Kullman 2002, Klanderud & Birks 2003, Peñuelas and Boada 2003, Sanz-Elorza *et al*. 2003). Some of these European studies showed an upward movement of plant species, which has been attributed to climate change (Grabherr *et al.* 1994, Kullman 2002, Klanderud & Birks 2003).

The Alps

Grabherr and colleagues surveyed 26 summits of over 3,000 m above sea level (a.s.l) in the central Alps (western Austria and eastern Switzerland) in the summer of 1992. The data from this survey were then compared with historical records of cover and abundance of vascular plant species (Grabherr *et al*. 1994, 1995, Pauli *et al*. 1996, Gottfried *et al*. 1998). This showed an upward movement in the distribution of plant species. Working on the basis of 12 very precise historical records, they calculated the rate of upward movement of the nine fastest moving plant species to be between 1 - 4 m per decade, with the rest extending their upward distribution by less than one meter per decade (Grabherr *et al*. 1994). The historical records used for these calculations were collected between 1900 and 1920. The greatest increases in species richness were most pronounced at lower altitudes (Grabherr *et al*. 1994).

Further west in the Alps, Keller and colleagues were able to study a “unique 70 year data set of high-elevation permanent vegetation plots” in Schynige Platte in the Bernese Alps of Switzerland (Keller *et al.* 2000). They found that the probability of finding plant species which favour warmer conditions had increased since the 1930s, and they found a decrease in the number of species which prefer cooler conditions. These studies took place at altitudes above those where direct anthropogenic influences, such as livestock grazing, would have an effect (Keller *et al.* 2000). Also the change was found to be independent of changes in availability of nutrients, and so they concluded that changes in climatic conditions explained the changes seen in the vegetation. Their observations show close agreement with the upward migrations reported by Grabherr and colleagues.

Spain

Sanz-Elorza *et al*. (2003) investigated ’significant changes in vegetation’ over a 40 year period in the Peñalara massif (2430 m a.s.l) in central Spain. They found an upward movement of shrubs from lower levels into the Cryoro-Mediterranean sub-alpine zone. This movement is possibly due to increases in temperature, changes in monthly rainfall patterns and reductions in snow cover. However other factors were also seen as being important, such as changes to the grazing regime in the 19th century.

In a similar study in North East Spain, Peñuelas and Boada (2003) showed a “progressive replacement of cold-temperate ecosystems by Mediterranean ecosystems”, with a ca. 70 m upward altitudinal shift of beech (*Fagus sylvatica*). Here again changes in grazing regime and shepherding practice, as well as climatic change, have had an effect on the observed shifts in vegetation zones (Peñuelas and Boada 2003). This shows that the relationship between shifts in vegetation zones and climate change can be part of more complex interactions, which can include changes in land management practice.

Scandinavia

Similar upward movements of plant species have been observed by Klanderud and Birks (2003) in the Jotunheimen mountains of central Norway (61° N) at altitudes between 1500 m and the summits above 2000 m. They found an increase in species richness and distribution on 19 out of 23 mountains surveyed in 1998, when compared with detailed surveys carried out in 1930 – 31. No details are given about the four mountains where they do not report increases in species richness or distribution. The greatest increases were recorded in the east and at lower altitudes, with only slight changes in richness on windswept summits. A few species were reported to have decreased in frequency, these were species associated with late lying snow beds. However, Klanderud and Birks attribute this change to the effects of acid deposition, rather than climate change. They also report that some of the species most frequently found at high altitudes have "disappeared" from sites at lower altitude where they were previously recorded, but have increased in abundance at the highest altitudes. This they suggest may be due to the effects of strengthening competition. They considered the possible influence of other factors such as changes in grazing pressure, nitrogen deposition, and tourism, along with their interactions, but concluded climatic warming to be the major driver for the upward shifts of vegetation which they have reported (Klanderud & Birks 2003).

In the Scandes mountains of northern Sweden (63°26' N 13°06' E), Kullman (2002) used a combination of repeat surveying of historical records from 1955, and age determination of saplings to investigate changes in the range-margin of seven tree and shrub species. He found individual species moving between 120 and 375 m in altitude and a rise in the overall forest tree line of between 100 m to 150 m. By examining the age structure of the saplings, Kullman determined that they had established since 1987. This coincides with a period of warm summers and mild winters in that area (Kullman 2002). The saplings observed showed unchecked height increments, which is not characteristic of exposed high altitude saplings. Normally such saplings would exhibit stunted growth due to repeated winter dieback of the shoots (Grace 1997). It is also notable that dwarf shrubs such as *Vaccinium myrtillus*, *Empetrum hermaphroditum* and *Betula nana* did not extend their altitudinal ranges in the same manner. In contrast, in the more oceanic Jotunheimen mountains of Norway, Klanderud and Birks (2003) did find *V. myrtillus* had expanded its altitudinal range. This suggests that not all plant species will respond to global climatic change in the same way and at the same rates between and within sites.

Australia

It has been difficult to find similar studies from mountain areas outside Europe. Interestingly, a study from Australia has shown a downward movement of alpine vegetation. Kirkpatrick and co-workers, by analysing photographs taken between 950 m and 1014 m a.s.l. in 1989 and 2000 on the summit of Hill One, in the south of Tasmania, found that sub alpine "bolster heath" had retreated down slope and was being replaced by "Alpine heath" plants. This downward retreat of the bolster heath was attributed to increased exposure to south-westerly winds in winter (Kirkpatrick *et al.* 2002). Tasmania, being an island, is subject to strongly oceanic climatic conditions which are much closer to Scottish conditions than the Alps.

Scotland

Unfortunately, in Scotland there is little evidence of the impact of climate change on the altitudinal range of plant species. This is largely due to relatively few early published botanical surveys of the Scottish Highlands providing reference points. The first systematic botanical survey of the Scottish uplands was not carried out until the turn of the 19^{th} and 20^{th} centuries by Robert Smith (Smith 1900). However, there is insufficient detail given in his published survey of the “North Perthshire District” (Smith 1900) for it to be possible to carry out a re-survey with any confidence. Unfortunately, details of Smiths own notes and records are unavailable. The next available historical botanical survey in the Highlands comes from Watt and Jones (1948), who were part of the Cambridge Botanical Expedition to the Cairngorms which took place over short periods during the summers of 1938 and 1939 (Watt & Jones 1948). The expedition based itself at Glenmore Lodge and the main survey area was between Coire Laogh Mór (north east) and Creag an Leth-choin (south west). The most detailed surveys were carried out in Coire na Ciste (referred to as Margaret’s Coffin) and Coire Cas. Unfortunately these areas were developed in the 1960’s to form the core of the Cairngorm ski area (for a description of changes in vegetation cover in Coire Cas between 1966 and 1987, see Bayfield 1996). Watt’s personal notes and records along with photographic plates are now archived in the Library at The University of Aberdeen. While these provide good botanical detail of areas outwith those affected by the skiing development, i.e. Ben Macdui and Braeriach, the spatial detail given is insufficient for a re-survey to be undertaken with confidence.

In the 1950s a systematic botanical survey of the Scottish Highlands was carried out McVean and Ratcliffe (1962). Unfortunately detailed records of this survey were not available.

Given this lack of long term botanical records, it is not surprising that there are no published studies of re-surveying historical surveys in Scotland. There is only one study showing an upward shift in vegetation. Bayfield and colleagues (1998) have reported that, over a 40 year period, *Pinus sylvestris* saplings have colonised areas up to 850 m a.s.l. in the Northern Corries of the Cairngorms. Following observations made by Pears (1967), they recorded the density of these saplings along fixed transects in 1984 and 1994, and found that there had been an increase in density in the second survey. The highest densities of saplings were found on the ridges between the corries at 650 m in the ski area. These findings are similar to those reported by Kullman (2002) in Sweden, however it is unclear whether this increase in saplings is due to climatic change or the reduction in grazing pressure from red deer (*Cervus elaphus*) (Bayfield *et al.* 1998).

The European studies detailed above are from areas which have a higher continentality index than Scotland (Figure 1.1). Continentality is a measure of how the climate of an area is affected by its remoteness from the oceans and oceanic air (Conrad 1964). The most often quoted indicator is the difference between average prevailing January and July temperatures.

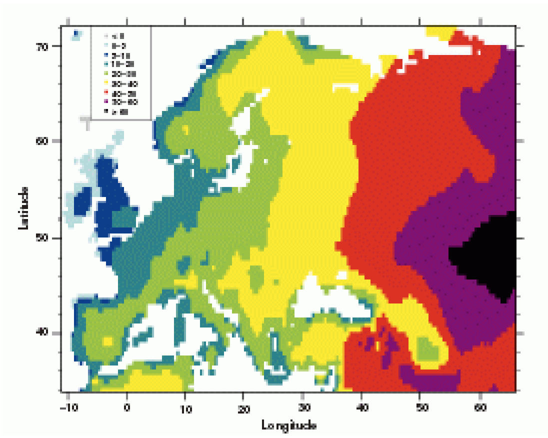


Figure 1.1. Conrad's index of continentality based on *European Gridded Climatology for 1961 -1990* (Hulme *et al.* 1995), taken from Crawford (2000). Areas nearest the oceans with low continentality have a low annual temperature range and those further away have a high annual temperature range.

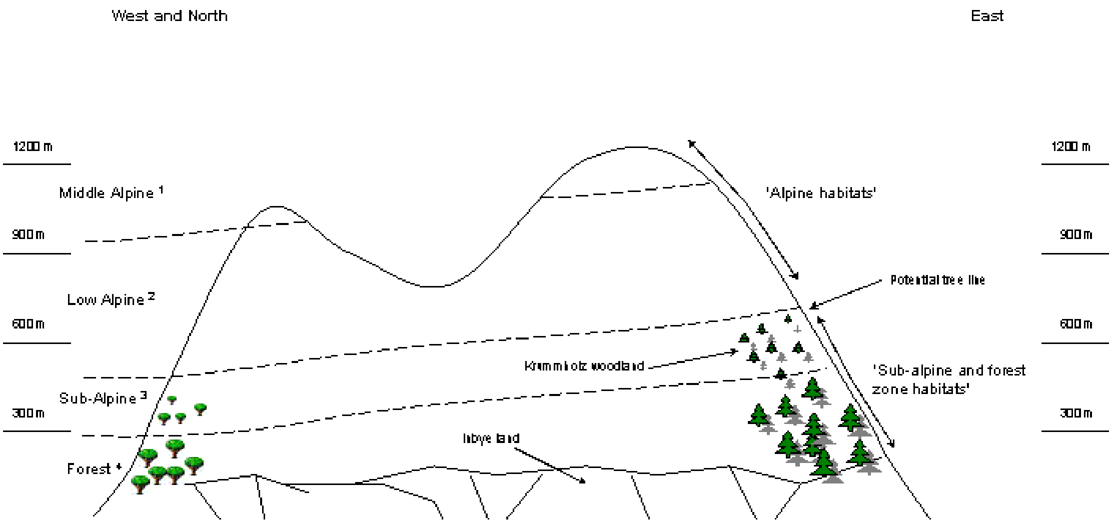
While the Jotunheimen mountains of Norway are climatically closer to Scotland than the Alps, they are still more continental than the Grampian mountains in Scotland. The results of Klanderud and Birks (2003) show a distinct trend with increasing change in species and species richness from west to east, suggesting that continentality may be a factor. Unfortunately, they did not have sufficient data to investigate this fully (Klanderud pers. comm.). This would suggest that predictions for Scotland based on these studies should be treated with caution, as the Scottish climate has a strong oceanic rather than continental influence. With the changes in climate predicted with global warming, the western and northern regions of Europe will become increasing oceanic (Crawford 2000).

1.2. Vegetation zonation in the Scottish mountains

It has long been recognised that the vegetation of the Scottish Highlands can be described according to altitudinal zonation (Smith 1900, Smith 1911, Matthews 1937, Watt & Jones 1948, Poore & McVean 1957, McVean & Ratcliffe 1962, Burnet 1964, Ratcliffe & Thompson 1988, Pearsall 1989, Brown *et al*. 1993). For example zones have been classified either side of the potential Scottish tree-line with the montane zone above and the submontane zone below (Brown *et al*. 1993). The montane zone is also referred to as the "alpine" or "arctic-alpine" zone by a number of authors (Thompson & Brown 1992, Thompson *et al*. 1995, Nagy 1997, Gordon et *al*. 1998, Gordon et *al*. 2002 etc.). Horsfield and Thompson (1996) simplify this by recommending that, in Scotland, the area below the potential tree-line be referred to as sub alpine and forest zone habitats (these are the equivalents of the European Sub Alpine and Forest zones) and above the tree-line as alpine habitats (equivalent to the European Low and Middle Alpine zones), see Figure 1.2.

The most obvious vegetation zone boundary in mountain areas, which even the lay person can recognise easily, is the tree-line. However, the ecological definition of what constitutes a tree-line is rather more complex (see Körner (1998) for a more detailed discussion of this point). In the context used here, the tree-line can be defined as the upper altitudinal boundary at which a forest or patches of forest grows, or in most of Scotland, would grow if it still existed. At the upper edge of this boundary most species of tree show stunted deformed growth, often referred to using the German term *krummholz* (Grace 1989).

In Scotland, Grace (1997) estimates that the potential tree-line is at its highest at *ca*. 620 m a.s.l. at Creag Fhiaclach (NH895055) in the Cairngorms, although other authors suggest it maybe higher (Pears 1967, Pears 1968, Horsfield & Thompson 1996). It declines to *c*. 520 m a.s.l. in the north west Highlands and is considered to be close to sea level in the most exposed areas of the northwest coast (Brown *et al*. 1993). In global terms this is an anomalously low tree line and is thought to be mainly due to the harsh wind climate experienced in the Scottish uplands (Grace 1989, 1990, 1997, Grace & Norton 1990, Körner 1998).



1 Grasses, sedges and rushes with moss, lichen and rock.
2 Wind clipped, prostrate ericaceous dwarf-shrubs, dwarf-herbs, moss carpets and snow-bed grassland.
3 Woods of birch, hazel and Scots pine and tall scrub (very localised); ericaceous dwarf-shrub heaths and tall herbs.
4 Woods Scots pine, oak ash and alder; ericaceous dwarf-shrub heaths, grassland and bracken.
Some vegetation types are azonal and cut across the altitudinal zones, i.e. blanket bogs, grasslands and flush-mires.

(After Horsfield & Thompson 1996)

Figure 1.2. Diagram indicating the altitudinal ranges of Scottish vegetation zones, these are lower in the north-west and far north where exposure is higher (on the left), and at higher altitudes in the east (on the right). Continental European terms are given on the left and Horsfield and Thompson's (1996) recommended terms for Scotland on the right.

Above the potential tree-line in Scotland, vegetation is dominated by dwarf shrubs which become increasingly prostrate due to wind clipping. At *c*. 800 m a.s.l. there is a transition from wind clipped *Calluna* heath to montane heath, and towards the summits *Racomitrium* heath can become dominant (referred to as the Upper Arctic-Alpine Zone by Poore & McVean 1957). On north, northeast or southeast facing slopes late laying snow beds can be found as low as 800 m a.s.l. (Watson *et al*. 1994). Within these there are broad vegetation types, some of which can be considered to be at risk from climatic change, in particular snow bed vegetation.

Most authors (Poore & McVean 1957, McVean & Ratcliffe 1962, Burnet 1964, Pearsall 1989, Thompson & Brown 1992, Brown *et al*. 1993, Thompson *et al*. 1995, Nagy 1997, Gordon et *al*. 1998, Gordon et *al*. 2002 etc.) note that these vegetation zones occur at lower altitudes in Scotland than their continental European equivalents. This is probably due to the oceanic nature of the Scottish climate, which is at the extreme end of several European environmental gradients (Nagy 1997). The Grampian mountains, which are the most continental area of the Scottish Highlands, are "highly oceanic on the European scale" (Nagy 1997; see also Figure 1.1). The Scottish winters are milder and wetter, the summers are cooler and wetter, and the wind climate is also far harsher than in most of continental Europe. The only mountain area of northern Europe which experiences a similarly oceanic climate to Scotland is the south west coast of Norway. Therefore, the nearest equivalent European vegetation zones to those in Scotland can be found in Norway. The Scottish submontane zone is the equivalent of the Norwegian subalpine forest zone, and the montane zone above the potential Scottish tree-line is the equivalent of the Norwegian lower and middle alpine zones (Brown et al. 1993).

1.3. Description of climate in the Scottish Highlands

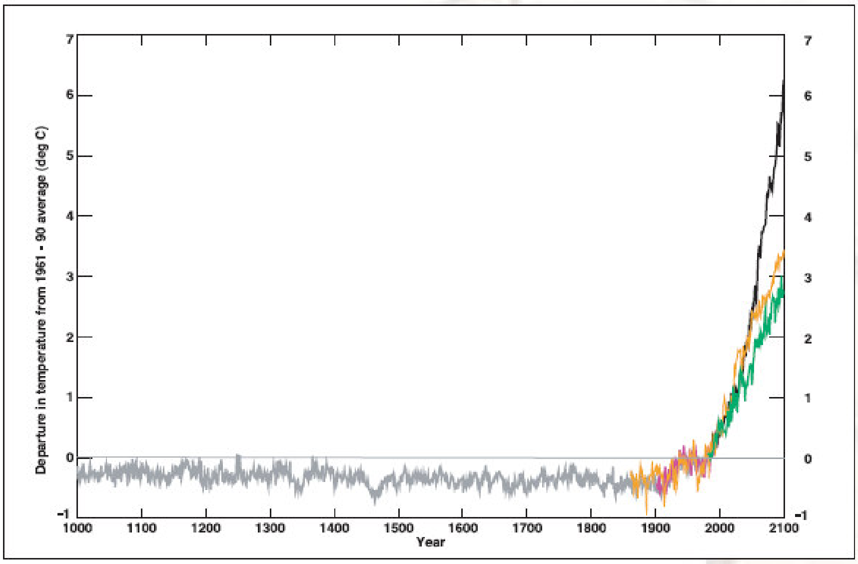
Scotland has a maritime or oceanic climate and is therefore described as having high oceanicity or low continentality. As stated above continentality is a measure of how the climate of an area is affected by its remoteness from the oceans and oceanic air (Conrad 1964). By comparison oceanicity is the effect of maritime influences on a climate (Allaby 1994). Oceanic climates are characterised by having a low annual temperature range, whereas continental climates have a wide annual temperature range. This can have important ecological effects, as plants are highly sensitive to the effects of this oceanicity, such as changes in temperature and rainfall gradients, the length and variability of the growing season (Crawford 2000).

Added to this are the climatic effects due to altitudinal gradients, which in Scotland are particularly steep and can have significant effects even at modest altitudes (Harrison & Kirkpatrick 2001). Scotland has a very high lapse rate (the rate at which temperature drops as altitude is gained) which is strongly influenced by oceanic effects (Pepin 2001) so that lapse rates change at a different rate to those in more continental areas. In Scotland lapse-rates are typically 10.0-10.5˚C km^{-1}, whereas in continental areas lapse-rates are typically 6.0˚C km^{-1} (Harding 1978, Harrison 1994, Harrison 1997). Also, the relationship between the levels of summer warmth (often expressed in degree days) and altitude is not linear (Parry 1976), and even small changes in temperature can have a larger effect in the uplands than in the lowlands. These are issues which should be borne in mind when considering the potential effects of climatic change in Scotland.

1.4. Climate change

1.4.1. Global climate change

There is increasing evidence that the global climate is changing, with a global temperature rise of about 0.6℃ at the Earth surface over the last 100 years (Houghton *et al*. 1996, IPCC 2000, IPCC 2001, Jones *et al*. 2001). Much of this change has been attributed to increasing concentrations of greenhouse gases, such as carbon dioxide (CO_2), produced by human activities. A number of models have been developed to predict possible climate change scenarios according to relative levels of greenhouse gas emissions (Collins *et al*. 2001, Durman *et al*. 2001, Hulme & Jenkins 1998, Hulme *et al*. 2002, Mitchell *et al*. 1999, Jones & Reid 2001, Wood *et al*. 1999). See Figure 1.3. These models predict a possible mean rise in global temperatures of between 1.5℃ and 5.8℃ over the next century (IPCC 2001).



Showing departure in temperature from 1961 – 90 average (deg C) ranging from -1 to 7 on Y axis and years from 1000 to 2100 (AD) on X axis.

= reconstructed from environmental data for 1000 to 1980;
= observed from thermometers for 1901 to 1999;
= a single model simulation for 1860 to 2100 with "observed" natural and anthropogenic forcings to 2000 and then a mid-range emissions scenario from 2000 to 2100;
= a single model simulation for 1981 to 2100 using a low emissions scenario;
= a single model simulation for 1981 to 2100 using a high emissions scenario.
All simulations were carried out using the HadCM3 model. [Source: adapted from IPCC, 2001]

Figure 1.3. Reconstructed and recorded past temperatures, and modelled future temperature for the Northern Hemisphere shown as anomalies from a 1961 – 1990 temperature average. The reconstructed temperatures have been estimated from “proxy” climate indicators such as tree: rings, corals, ice cores, lake and ocean sediments, borehole measurements, historical documents and glacier moraines etc. (IPPC 2001) (figure taken from Hulme et al. 2002).

1.4.2. Predicted climate change scenarios for Scotland

The most recent predictions suggest that the average annual temperature in the Scottish Highlands may increase by between 1℃ and 2℃ by 2050 (Harrison *et al*. 2001, Hulme & Jenkins 1998, Hulme *et al*. 2002). Using a number of climate models developed by the Hadley Centre for Climate Prediction and Research (Hulme *et al*. 2002), the UK Climate Impacts Programme (UKCIP) has developed possible future climatic scenarios for the UK (UKCIP02). These are based on the estimated impacts of global emissions scenarios resulting from alternative paths of world development (Hulme *et al*. 2002). One major uncertainty in the climate models is the fate of the “thermohaline circulation” (THC), i.e. the Gulf Stream, which some models predict may weaken or shut down entirely in the near future. Should this occur, northwest Europe could experience cooling by up to 5°C within the space of a few decades (Hulme *et al*. 2002).

The UKCIP scenario predictions have a 50 km grid resolution, but there are still large uncertainties associated with these predictions. UKCIP02 does give an assessment of confidence in its predictions, however it should be noted that these confidence levels are qualitative and not quantitative (Hulme *et al*. 2002). In the following pages, the high emissions scenario for the 2050s was used where available, this is also similar to the medium emission scenario for the 2080s.

Temperature

As shown in Figure 1.4, the predicted increases in average daily temperatures in Scotland over the next 50 years are by up to +1.63°C in winter and + 2.31°C in summer using the UKCIP high emissions scenario. The high emissions scenario is based on there being an increase in concentration of CO_2 to double that of levels of pre-industrial levels by 2045.
Unpredictable or uncertain changes, such as volcanoes or solar changes in radiation, were not considered. The UKCIP give these predictions a high relative level of confidence.

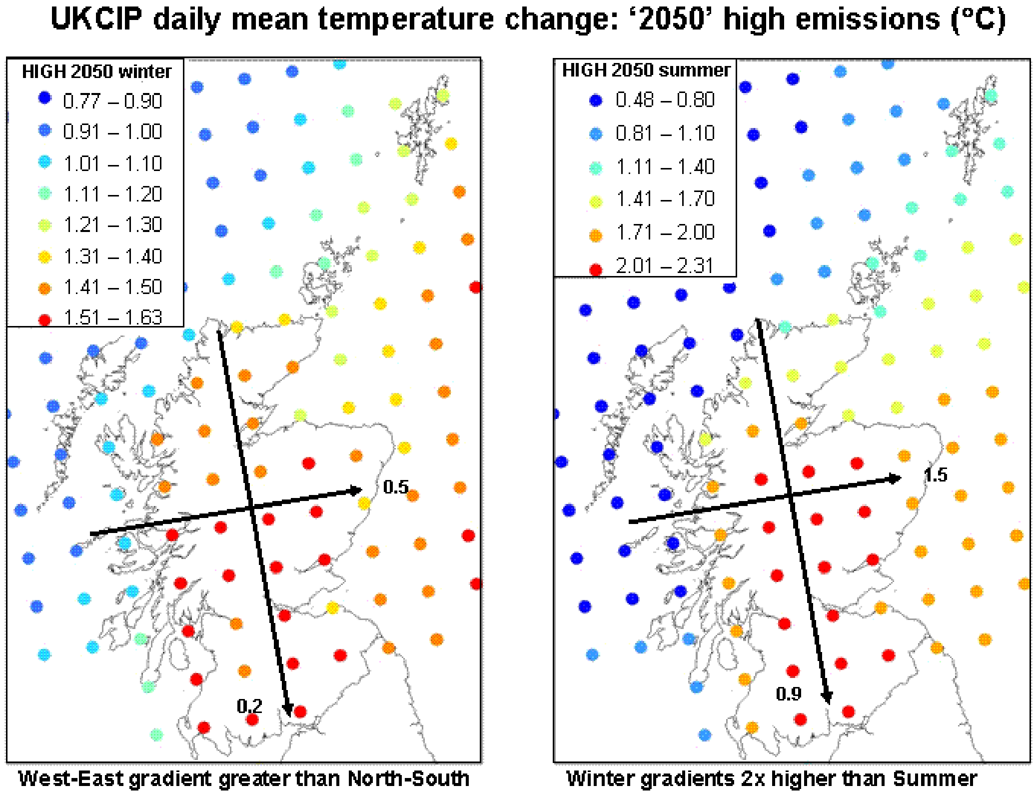


Figure 1.4. Predicted changes in daily mean temperatures (˚C) for Scotland over the next 50 years, showing an increase of up to 2.3℃ by the 2050s (source: UKCIP).

Precipitation

Seasonal predictions for relative changes in precipitation in Scotland are shown in Figure 1.5. These show a predicted decrease in summer rainfall of up to 24% in the high emission scenario by the 2050s. Winter precipitation is predicted to increase by up to 22% by 2050, with possibly the largest increase in the east. UKCIP's relative confidence level for the wetter winters is given as "high", but the relative confidence level for the drier summers is given as "medium". This is one of the changes from the UKCIP98 which was predicting wetter summers.

Winter snowfall (Figure 1.6) is predicted to decrease in Scotland by the 2050s by up to 65%, with the largest decrease in the east. The UKCIP gives a relatively high confidence level for "significant" declines in snowfall everywhere in the UK.

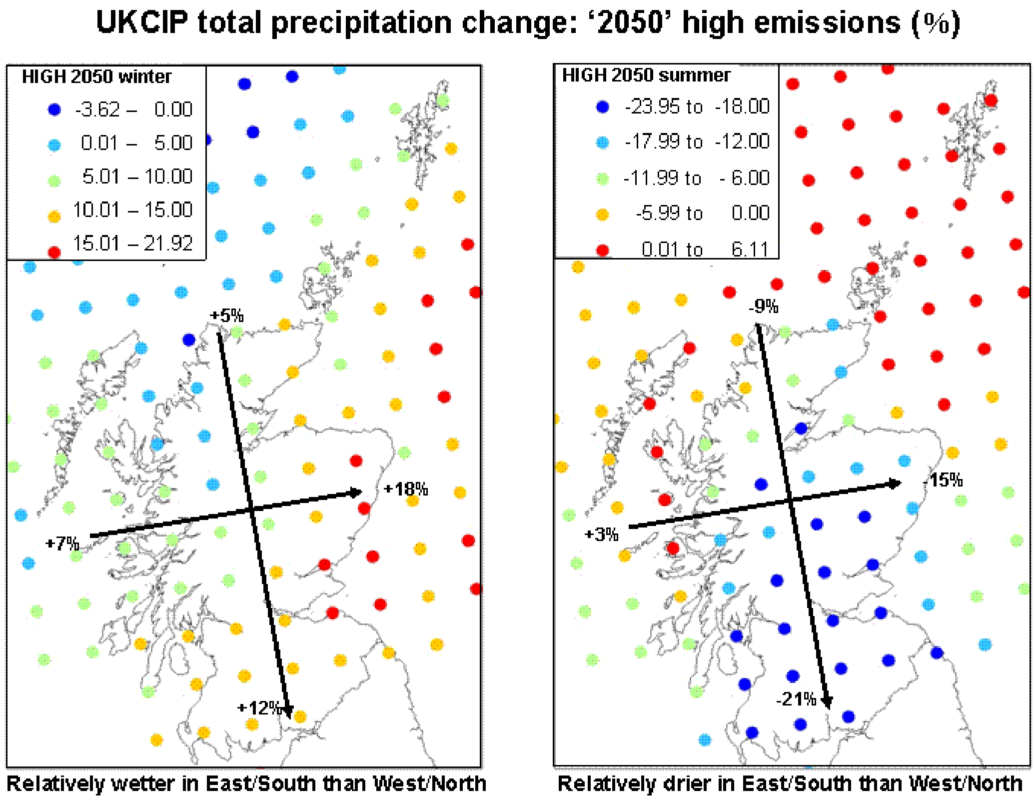


Figure 1.5. Predicted percentage changes in precipitation for Scotland over the next 50 years, showing a decline of up to 24% in summer and an increase of up to 22% in winter in the high emission scenario. (source UKCIP).

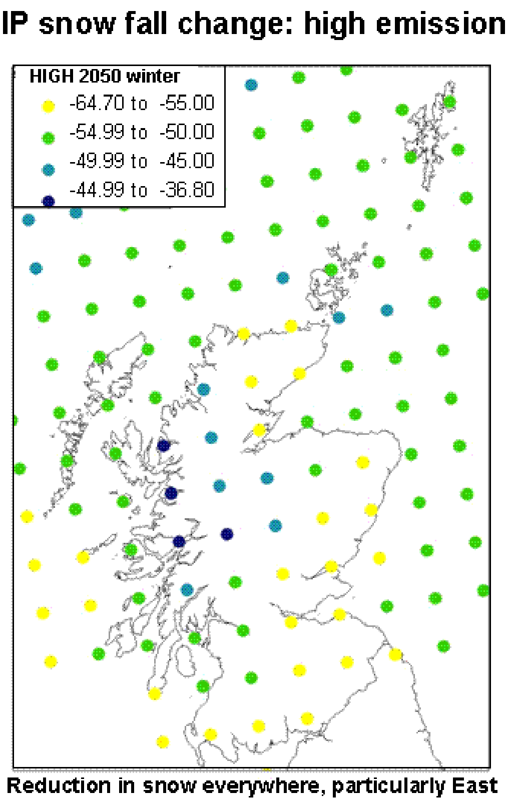


Figure 1.6. Predicted percentage changes in average winter snowfall for Scotland in the 2050s showing a reduction of up to 65% using the UKCIP high emissions scenario. (source: UKCIP).

Wind speed

The predicted changes in daily mean wind speed for Scotland by the 2080s are very small, between ± 3% for the annual average with slight increases in spring and slight decreases in summer and autumn, while winter remains within the “natural” variability (UKCIP02). The authors emphasize that, due to inconsistency between different models as well as the physical representation within the core model (HadRM3), they are unable to attach any level of confidence to the predictions of wind speed (Hulme *et al*. 2002).

Diurnal temperature range

Diurnal temperature range, the difference in temperature between day and night, is predicted to increase in Scotland by up to 1℃ in summer by the 2080s, with a slight decrease in winter and smaller increases in other seasons. UKCIP02 give a low level of confidence for this prediction.

1.5. Approach, hypotheses and thesis plan

Given the lack of suitable historical botanical surveys which could be used to investigate the potential changes in Scottish mountain vegetation due to global climate change over the past century, there is a need to find a different approach. A two pronged approach was taken:

Firstly, it was necessary to collect information on the potential for seed to move from lower vegetation zones to higher levels under predicted climate change. Secondly, it was necessary to determine if an increase in mean temperature, as predicted by the climatic models, would affect the strength of interactions between plants, i.e. any change in the level of competition.

1.5.1. Hypotheses

To investigate the dispersal limitations of mountain plant species, the following questions need to be addressed:

- Is there sufficient upward seed movement to enable an upward migration of plants?
- Is there seed in the seedbank which could germinate and colonise higher vegetation zones?
- Has the nature of the seedbank changed over recent decades?

To investigate the competitive interactions between plants at higher temperatures, the following questions were posed:

- Would an increase in temperature change the balance from facilitation (potential advantages of having neighbours, e.g. shelter, outweighing the disadvantages of increased competition) to competition at high altitudes?
- Is temperature a more important ecological factor than wind in the Scottish alpine zone?

1.5.2. Brief outline of experimental approach – layout structure

In order to address the questions posed above with regard to the effects of potential climatic change on mountain vegetation in Scotland, the following two studies were undertaken.

Chapter 2: Potential for plants to move in a changing climate – A study of mountain vegetation and seed dispersal.

To investigate the dispersal limitations of mountain plant species, soil cores were taken at 50 m altitudinal intervals along four transects in the Grampian mountains of Scotland, to measure the seed bank present. Current seed rain was recorded at the same sites, using pitfall seed traps, over a two year period. A vegetation survey was also carried out at all trapping stations, to determine the current surface vegetation present. Current seed rain, surface vegetation and the seed bank were compared to seek evidence for a potential shift in vegetation.

Chapter 3: Effects of environmental manipulation of local climate on plant interaction.

To test whether an amelioration of harsh environmental conditions, simulating the effects of predicted climate change, would alter the balance between competition and facilitation in arctic/alpine plant communities, an experiment was set up using passive warming devices. Open Top Chambers (OTCs), simple wind shelters and control treatments were set up on Glas Tulaichean in the Glenshee area at 1000 m a.s.l., using *Carex bigelowii* and *Alchemilla alpina* as target plants. These two species where chosen as they both occur at the field site, are easy to use, and are predicted to be vulnerable to global climate change (Berry *et al*. 2002, Berry pers com.). The target plants were transplanted into replicate environmental treatments, and, within each environmental treatment, they were planted with as well as without neighbours. The OTCs are designed to achieve a warming effect by reduction of wind speed and by acting as solar traps, in the same way as a greenhouse (Marion 1996). Measurements were taken of final above ground biomass of the target plants, as well as environmental variables (soil and air temperature, wind speed and direction, soil moisture and PAR), to determine if the warming provided by environmental treatments would be sufficient to increase levels of competition experienced by the target species, and whether temperature was a more important ecological factor than wind.

Chapter 4: Discussion

The thesis integrates the results of these two pieces of work with the relevant literature and in Chapter 4 discusses potential changes in community structure due to migration and changes in competition. The potential effects of the predicted changes in environmental factors on mountain plants and vegetation zones are also discussed, and compared with the findings of the two experimental studies. Possible improvements to work carried out and recommendations for further research are suggested.

References

Allaby, M. (1994) *Oxford concise dictionary of Ecology.* Oxford University Press, Oxford.

Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R. and Latour, J.B. (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, **8**, 390-407.

Bayfield, N.G. (1996) Long-term changes in colonization of bulldozed ski pistes at Cairn Gorm, Scotland. *Journal of Applied Ecology*, **33**, 1359-1365.

Bayfield, N.G., Fraser, N.M. and Calle, Z. (1998) High altitude colonisation of the Northern Corries of Cairn Gorm by Scots pine (*Pinus sylvestris*). *Scottish Geographical Magazine*, **114**, 172-179.

Berry, P.M., Dawson, T.P., Harrison, P.A. and Pearson, R.G. (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography*, **11**, 453-462.

Brown, A., Birks, H.J.B. and Thompson, D.B.A. (1993) A new biogeographical classification of the Scottish uplands. II. Vegetation - environment relationships. *Journal of Ecology*, **81**, 231-251.

Burnet, J.H. (1964) *The vegetation of Scotland.* Oliver and Boyd, Edinburgh and London.

Collins, M., Tett, S.F.B. and Cooper, C. (2001) The internal climate variability of HadCM3, a version of the Hadley Centre coupled model without flux adjustment. *Climate Dynamics*, **17**, 61-81.

Conrad, V. (1964) Usual formulas of continentality and their limits of validity. *Transactions of the American Geophysical Union*. **27**, 663-664.

Crawford, R.M.M. (2000) Ecological hazards of oceanic environments. *New Phytologist*, **147**, 257-281.

Durman, C.F., Gregory, J.M., Hassell, D.C., Jones, R.G. and Murphy, J.M. (2001) A comparison of extreme European daily precipitation simulated by a global and a regional climate model for present and future climates. *Quarterly Journal of the Royal Meteorological Society*, **127**, 1005-1015.

Ellis, N. (2004) *Climate Change Impacts: The rate of climate change*. Information Note Series. Scottish Natural Heritage.

Gordon, J.E., Dvorak, I.J., Jonasson, C., Josefsson, M., Kocianova, M. and Thompson, D.B.A. (2002) Geo-ecology and management of sensitive montane landscapes. *Geografiska Annaler Series a-Physical Geography*, **84A**, 193-203.

Gordon, J.E., Thompson, D.B.A., Haynes, V.M., Brazier, V. and Macdonald, R. (1998) Environmental sensitivity and conservation management in the Cairngorm Mountains, Scotland. *Ambio*, **27**, 335-344.

Gottfried, M., Pauli, H. and Grabherr, G. (1998) Prediction of vegetation patterns at the limits of plant life: A new view of the alpine-nival ecotone. *Arctic and Alpine Research*, **30**, 207-221.

Grabherr, G., Gottfried, M. and Pauli, H. (1994) Climate effects on mountain plants. *Nature*, **369**, 448.

Grabherr, G., Gottfried, M., Gruber, A. and Pauli, H. (1995) Patterns and current changes in alpine plant diversity. *In Arctic and alpine biodiversity* (eds F. S. Chapin and C. Körner), pp. 167-181. Springer-Verlag, Berlin.

Grace, J. (1989) Tree Lines. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **324**, 233-245.

Grace, J. (1990) Cuticular Water-Loss Unlikely to Explain Tree-Line in Scotland. *Oecologia*, **84**, 64-68.

Grace, J. (1997) The oceanic tree-line and the limit for tree growth in Scotland. *Botanical Journal of Scotland*, **49**, 223-236.

Grace, J. and Norton, D.A. (1990) Climate and growth of *Pinus sylvestris* at its upper altitudinal limit in Scotland - evidence from tree growth-rings. *Journal of Ecology*, **78**, 601-610.

Harding, R.J. (1978) The variation of the altitudinal gradient of temperature within the British Isles. *Geografiska Annaler Series A*, **60**, 43-49.

Harrison, P. A., Berry, P. M., and Dawson, T. P. (2001) Climate Change and Nature Conservation in Britain and Ireland: Modelling natural resource responses to climate change (the MONARCH project). UKCIP Technical Report. Oxford.

Harrison, S.J. and Kirkpatrick, A.H. (2001) Climate change and its potential implications for Scotland's natural heritage. In: *Earth Science and the Natural Heritage: Interactions and Integrated Management.* (eds J. E. Gordon and K. E. Leys), pp. 296-305. The Stationery Office, Edinburgh.

Horsfield, D. and Thompson, D. B. A. (1996) *The Uplands: guidance on terminology regarding altitudinal zonation and related terms*. Information and Advisory Note No. 26. SNH, Battleby.

Houghton, J.R., Meira Filho, L.G., Callander, B.A., Harris, N., Kattenberg, A. and Maskell, K. (1996) *Climate change 1995*. Cambridge University Press, Cambridge, UK.

Hulme, M. and Jenkins, G. J. (1998) *Climate change scenarios for the UK: scientific report. No.1*. UKCIP, Technical Report, Norwich, Climatic Research Unit.

Hulme, M., Conway, D., Jones, P.D., Jiang, T., Barrow, E.M. and Turney, C. (1995) Construction of a 1961-1990 European climatology for climate change modelling and impact applications. *International Journal of Climatology*, **15**, 1333-1363.

Hulme, M., Jenkins, G. J., Lu, X., Turnpeny, J. R., Mitchell, T. D., Jones, R. G., Lowe, J., Murphy, J. M., Hassell, D., Boorman, P., McDonald, R., and Hill, S. (2002) *Climate change scenarios for the United Kingdom: The UKCIP02 scientific report*. p. -120. Norwich, UK, Tyndall Centre for Climate Change Research, School of Environmental Science, University of East Anglia.

Huntley, B., Ashcroft, D.R., Berry, R.M., Cramer, W.P. and McDonald, A.P. (1995) Modelling present and potential future ranges of some European higher plants using climatic response surfaces. *Journal of Biogeography*, **22**, 967-1001.

IPCC (2000) *Special report on emissions scenarios (SRES): A special report of Working Group III of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.

IPCC (2001) *Climate change 2001: the scientific basis*. Cambridge University Press, Cambridge, UK.

IPCC (2001) Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change [Houghton, J.T.,Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, and C.A. Johnson (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 881pp.

Jones, P.D. and Reid, P.A. (2001) Assessing future changes in extreme precipitation over Britain using regional climate model integrations. *International Journal of Climatology*, **21**, 1337-1356.

Jones, P.D., Osborn, T.J. and Briffa, K.R. (2001) The evolution of climate over the last millennium. *Science*, **292**, 662-667.

Keller, F., Kienast, F. and Beniston, M. (2000) Evidence of response of vegetation to environmental change on high-elevation sites in the Swiss Alps. *Regional Environmental Change*, **1**, 70-77.

Kirkpatrick, J.B., Bridle, K.L. and Lynch, A.J.J. (2002) Changes in alpine vegetation related to geomorphological processes and climatic change on Hill One, Southern Range, Tasmania, 1989-2000. *Australian Journal of Botany*, **50**, 753-759.

Klanderud, K. and Birks, H.J.B. (2003) Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene*, **13**, 1-6.

Körner, C. (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, **115**, 445-459.

Kullman, L. (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, **90**, 68-77.

Matthews, J.R. (1937) Geographical relationships of the British flora. *Journal of Ecology*, **25**, 1-90.

McVean, D.N. and Ratcliffe, D.A. (1962) *Plant communities of the Scottish Highlands: A study of Scottish mountain, moorland and forest vegetation.* HMSO, London.

Mitchell, J.F.B., Johns, T.C., Eagles, M., Ingram, W.J. and Davis, R.A. (1999) Towards the construction of climate change scenarios. *Climatic Change*, **41**, 547-581.

Nagy, J. (1997) Plant Biodiversity in Scottish Alpine Vegetation: a review and research needs. *Botanical Journal of Scotland*, **49**, 469-477.

Parry, M.L. (1976) The significance of the variability of summer warmth in upland Britain. *Weather*, **31**, 212-217.

Pauli, H., Gottfried, M. and Grabherr, G. (1996) Effects of climate change on mountain ecosystems - upward shift of alpine plants. *World Resource Review*, **8**, 382-390.

Pears, N.V. (1967) Present Tree-Lines of the Cairngorm Mountains, Scotland. *Journal of Ecology*, **55**, 815-830.

Pears, N.V. (1968) The natural altitudinal limit of forest in the Scottish Grampians. *Oikos*, **19**, 71-80.

Pearsall, W.H. (1989) *Mountains and Moorlands.* Bloomsbury Books, London.

Pearson, R.G., Dawson, T.P., Berry, P.M. and Harrison, P.A. (2002) SPECIES: A Spatial Evaluation of Climate Impact on the Envelope of Species. *Ecological Modelling*, **154**, 289-300.

Peñuelas, J. and Boada, M. (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biology*, **9**, 131-140.

Pepin, N. (2001) Lapse rate changes in northern England. *Theoretical and Applied Climatology*, **68**, 1-16.

Poore, M.E.D. and McVean, D.N. (1957) A new approach to Scottish mountain vegetation. *Journal of Ecology*, **45**, 401-439.

Ratcliffe, D.A. and Thompson, D.B.A. (1988) The British uplands: their ecological character and international significance. In: *Ecological Change in the Uplands* (eds M. B. Usher and D. B. A. Thompson), pp. 9-36. Blackwell Scientific Publications, Oxford.

Sanz-Elorza, M., Dana, E.D., González, A. and Sobrino, E. (2003) Changes in the High-mountain Vegetation of the Central Iberian Peninsula as a Probable Sign of Global Warming. *Annals of Botany*, **92**, 273-280.

Smith, R. (1900) Botanical survey of Scotland. II North Perthshire District. *The Scottish Geographical Magazine*, **16**, 441-467.

Smith, W.G. (1911) Arctic-alpine vegetation. In: *Types of British vegetation.* (ed A. G. Tansley), pp. 288-329. Cambridge University Press, Cambridge.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, .F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L. and Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145-148.

Thompson, D.B.A. and Brown, A. (1992) Biodiversity in montane Britain: habitat variation, vegetation diversity and some objectives for conservation. *Biodiversity and Conservation*, **1**, 179-208.

Thompson, D.B.A., Macdonald, A.J., Marsden J.H. and Galbraith, C.A. (1995) Upland Heather Moorland in Great-Britain - a Review of International Importance, Vegetation Change and Some Objectives for Nature Conservation. *Biological Conservation*, **71**, 163-178.

Watson, A., Davison, R.W. and French, D.D. (1994) Summer snow patches and climate in Northeast Scotland, UK. *Arctic and Alpine Research*, **26**, 141-151.

Watt, A.S. and Jones, E.W. (1948) The ecology of the Cairngorms. Part 1. The environment and the altitudinal zonation of the vegetation. *Journal of Ecology*, **36**, 283-304.

Wood, R.A., Keen, A.B., Mitchell, J.F.B. and Gregory, J.M. (1999) Changing spatial structure of the thermohaline circulation in response to atmospheric CO_2 forcing in a climate model. *Nature*, **399**, 572-575.