

Movement of mountain vegetation zones under predicted climatic change

Kim Harding

The Northern Studies Centre

2002

k.harding@abdn.ac.uk

Keywords: mountain, vegetation zones, alpine plants, plant communities, seeds, climate change, Scotland.

Abstract

Scotland has over 90% of the UK's montane (alpine) habitat. These areas contain important populations of relic arctic, alpine and endemic plants, which also support important bird populations, all of which are of high conservation value. Within these areas, natural zonation of vegetation can be seen at different altitudes. This zonation is largely due the effects of temperature and winter wind speed (which influences snow lie and therefore exposure to low temperatures and wind abrasion). It is therefore possible that plant communities in mountain areas will be sensitive to the effects of long term climatic change. There is increasing evidence that the global climate is changing, with a global temperature rise of about 0.6°C over the last 100 years. Much of this change has been attributed to increasing concentrations of greenhouse gases, such as carbon dioxide (CO₂), produced by human activities. A number of models has been developed to predict possible climate change scenarios according to relative levels of greenhouse gas emissions. The most recent predictions suggest that the average annual temperature in the Scottish Highlands will increase by between 1° C and 2° C by 2050. If the predicted temperature increase occurs, it could result in pressure for an upward altitudinal shift of vegetation zones by 100 to 200m, as altitudinal zonation is partly temperature driven. What are the potential effects of climate change on Scottish montane plant communities? To try and tackle this question I have come up with three experiments: a chamber experiment, a transplant experiment, and a seed trapping experiment

Introduction:

Scotland has over 90% of the UK's montane (alpine) habitat; including a mixture of dwarf-shrub heath, moss heath, grasslands, fellfields, snowbeds and rock communities. Many of these plant communities are near natural and so have a high conservation value. These areas also contain important populations of relic arctic, alpine and endemic plants, as well as supporting important bird populations. Natural altitudinal zonation of vegetation can be seen in the Scottish highlands and has been described by a number of authors (Smith 1900,

Watt & Jones 1948, Poore & McVean 1957, Pearsall 1989, Thompson & Brown 1992, Brown et al. 1993, Gordon et al. 1998, etc). Watt and Jones (1948), working in the Cairngorms, describe three main "climatically limited" vegetation zones, dominated by *Calluna*, *Empetrum/Vaccinium* and *Juncus triffidus* (in order of increasing altitude). The two main factors they considered to be driving the zonation of these plant communities were altitude and exposure/snow cover. Poore and McVean (1957) covered a wider area of the Highlands in their "new approach to Scottish mountain vegetation". They described a similar altitudinal zonation to Watt and Jones (1948) but also recognised the lowering of vegetation zones, which occurs towards the north and west with increasing effects of oceanicity and moisture. This early work shows that climate has a strong influence on vegetation zonation, with two important factors being temperature and winter wind speed (which influences snow lie and therefore exposure to low temperatures and wind abrasion).

There is increasing evidence that the global climate is changing. There has been a global temperature rise of about 0.6°C over the last 100 years, with 1998 the single warmest year in the 142 year global instrumental record (Hulme et al. 2002). Much of this change has been attributed to positive radiative forcing caused by increasing concentrations of greenhouse gases, such as carbon dioxide (CO₂), produced by human activities (IPPC 1995). As climate has an important role in determining the altitudinal zonation of vegetation, it is possible that high altitude plant communities in mountain areas will be sensitive to the effects of long term climatic change (Grabherr & Pauli 1994, Klanderud & Birks 2003).

In order to assess the likely impacts of climate change on the United Kingdom, the UK Climate Impacts Programme (UKCIP) was formed. This programme has developed models that have predicted four possible climate change scenarios according to relative levels of greenhouse gas emissions: Low Emission, Medium-Low Emission, Medium-High Emission and High Emission. Predictions from the UKCIP 2002 report (Hulme et al. 2002) suggest that mean annual temperature in the Scottish Highlands will increase by between 1° C (Low Emission) and 2° C (High Emissions) over the next 50 years. Predictions for the wind climate are far less clear, but suggest that, while southern and central Britain will experience stronger winds, in Scotland wind strength will be no greater than at the present time. If, as predicted, there is an increase in temperature of between 1° C and 2° C, this could mean there is the possibility for an upward altitudinal shift of vegetation zones by 100 to 200m, as the altitudinal zonation is partly temperature driven.

As altitude increases, temperature decreases. In Scotland this rate of change (lapse rate) is generally given as a decrease of 1° C for every 100 m increase in altitude. This leads to an environment that is increasingly hostile for plant growth and reproduction with increasing altitude. It is likely that the upper altitudinal limits of many plants are determined by their tolerance of abiotic

factors (temperature or wind exposure), with biotic factors (i.e. competition) becoming increasingly important at lower altitudes. Most high altitude plant species are adapted to slow growth and are less competitive, which results in a trade-off between competitive ability and survival in the increasingly severe abiotic environment. This may determine the altitudinal range over which a species occurs. In plant communities of generally slow growing species that occur in areas with severe abiotic conditions, competition may be limited, and so facilitation may play a more important role in community structure. If climatic change leads to an amelioration of the severity of the abiotic environment at high altitudes, this may in turn lead to an increase in competition among species and the possible invasion of species currently limited to lower altitude sites. The importance of facilitation may also be reduced for some high altitude communities.

So, what are the potential effects of climate change on Scottish montane plant communities?

To try and tackle this question I have come up with a couple experiments:

1. a Open Topped Chamber field experiment and
2. a seed trapping and seed bank trial

1. Chamber experiment.

Hypothesis: the effect of climate change were to increase competition in high altitude communities where currently facilitation may be more important.

Introduction:

Most high altitude plant species are adapted to slow growth and are less competitive, which results in a trade-off between competitive ability and survival in the increasingly severe abiotic environment. This may determine the altitudinal range over which a species occurs. In plant communities of generally slow growing species that occur in areas with severe abiotic conditions, competition may be limited, and so facilitation may play a more important role in community structure.

There is increasing evidence that the global climate is changing. There has been a global temperature rise of about 0.6°C over the last 100 years, with 1998 the single warmest year in the 142 year global instrumental record (Hulme et al. 2002). Predictions from the UKCIP 2002 report (Hulme et al. 2002) suggest that the mean annual temperature in the Scottish Highlands will increase by between 1°C (under a Low Emissions scenario) and 2°C (High Emissions scenario) over the next 50 years. If climatic change leads to an amelioration of the abiotic environment at high altitudes, this may in turn lead to an increase in competition among species.

In this experiment summer temperature and wind exposure were manipulated during the growing season, in order to investigate the effects of climatic change on the magnitude of competition between species in a high altitude community. This were tested using neighbour removal experiments carried out under different climatic manipulations.

Study area:

This research was carried at 1000 m a.s.l. (grid reference NO048758), near the summit plateau of Glas Tulaichean (1051 m), in Scottish Highlands to the north-west of the Spittal of Glenshee. The underlying geology is Caenlochan Schist with Lamprophyre and Felsite intrusions (BGS 1989), which is acidic in nature. The area is designated a Site of Special Scientific Interest (international importance) and is a provisional Special Area of Conservation. The SSSI citation is for rare plant species growing on the cliff to the east of the site and states the site has “a representative range of summit vegetation, including montane heaths” (SNH file Ref: NO07/2). The summit vegetation consists of an area of extensive *Carex* - *Racomitrium* heath, vegetation below the summit is dominated by wind clipped *Vaccinium* and *Empetrum*.

Experimental set up:

In order to test the effects of an increase in temperature on competition in plant communities, eight Open Topped Chambers (OTC) modified from a standard design (Molau & Mølgaard 1996) and eight wind shelters were used to allow the climatic manipulations (see Figure 1). These OTCs have been shown to be effective at providing an analogue for climate warming (Hollister & Webber 2000). The chambers gave an increase in temperature, but at the same time reduced the level of wind exposure experienced by the plants. In order to isolate the effect of wind exposure a simple wind shelter was used (see Figure 2). Each OTC or wind shelter represented one experimental unit.

The OTCs and Wind Shelters have the advantage of being a robust, tried and tested design (Marion *et al.* 1997), and are relatively cheap. The wind shelters are a simpler design, 3mm thick Plexiglas strips 1 m in length and 20 cm height. The experiment, was set up in the summer of 2002 and will run for two further growing seasons. The chambers and shelters were to be used during the growing season, the original plan was for the chambers to be taken in for the winter period. However, as there was a early and heavy snow fall in October 2002 it was not possible to take the chambers in and so they were left in situ and monitored to see how much they effected the snow cover.



Fig. 1. An Open Topped Chamber (OTC) in use.

The two brown areas inside the chamber are the neighbours removed treatments, individual plants being studied are marked with red markers.

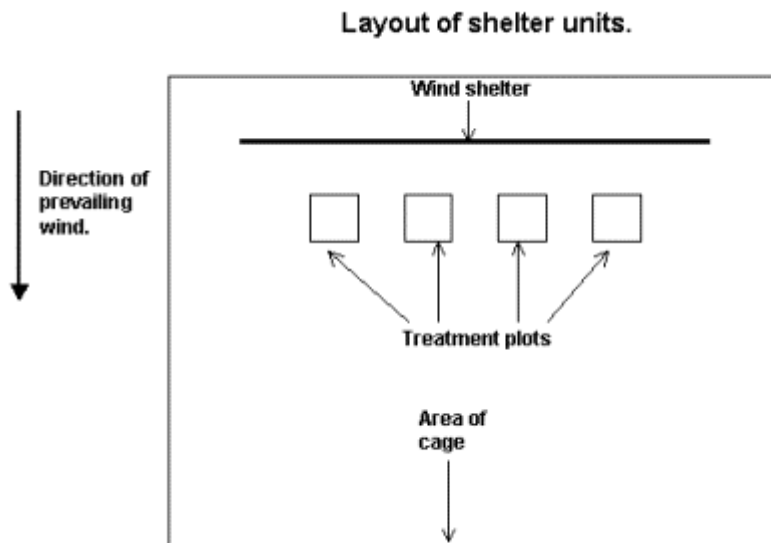


Fig. 2. An example of how the shelters were to be set up. The wind shelter is 1 m in length

Each chamber or shelter is an experimental unit providing the warming and/or shelter treatment. Each experimental unit contained four 10 cm x 10 cm plots which had both with and without neighbour treatments for each of the two species used (see below). There were eight replicates of each of the chambers, shelters and controls. This is a realistic number that allows for valid statistical assessments. To avoid disturbance from large herbivores or curious humans, simple mesh cages (approximately 1.3m long x 1m wide x 0.3m high) were used, to protect the shelters and controls (these cages were left in situ through the winter as they have little effect on wind climate and snow lay).

Treatments to applied:

Treatment	Neighbours
Warming and shelter (Chamber)	+
	-
Wind Shelter only (Shelter)	+
	-
No Warming or shelter (Control)	+
	-

Neighbour removal manipulations:

Two plant species were targeted, *Carex bigelowii* (Stiff sedge) and *Alchemilla alpina* (Alpine Lady's Mantel). *C. bigelowii* is a perennial clonal sedge with creeping rhizomatous growth (Brooker *et al.* 2002). *A. alpina* is a creeping herbaceous perennial, which occurs widely in upland Britain. Berry *et al* (2002) have suggested that the range of both these species may be affected by climate change.

Individuals of *C. bigelowii* and *A. alpina* were collected inwith the summit area, and were transplanted into 20 cm x 20 cm plots consisting of a matrix of existing vegetation. As far as possible the plants to be used for each replication were the same size and age. The plants will be tagged and numbered so that they can be easily found and identified. The plots were paired for each species, in one plot the target plant were left with neighbours and in the second all neighbouring plants, inwith a 10 cm radius of the target plant, were removed. The neighbouring plants were removed by manually clipping away all plants at ground level inwith the plot; this were repeated on monthly basis (or more often if needed) throughout the growing season. The below ground parts of the plants will not be removed, as this would disturb the root systems (Aarssen & Epp 1990). The edges around the “without neighbours” plot were cut straight down to sever roots or rhizomes from plants outwith the plot. Soil samples were take from both the with neighbours and no neighbours plots, at the end of the experiment, to check that the nutrient availability is constant.

The area within each chamber will divided into four plots (north, south, east and west), so that the position used for each treatment can be replicated twice, allowing a control for the effect of position within the chamber. The layout of the wind sheltered plots is shown in Figure 2 (see above), again the position used for each treatment can be replicated twice.

For *C. bigelowii*, number of leaves, length of longest leaf, culm height on flower stalk, amount of seed produced (i.e. number of nutlets) were measured (if produced). Leaf length and culm height were chosen because they give a measure of performance as they are significantly correlated with total tiller dry weight (Carlsson & Callaghan 1991). Measurements are taken at end of the growing season.

For *A. alpina*, 20-30mm lengths of rhizome with a single growing apex have been transplanted (Morecroft & Woodward 1996). Measurements to be made on *A. alpina* are, number of leaves (Kershaw 1960), numbers of flowers and amount of seed produced. Measurements of the leaves were taken at the beginning and end of the season and flowering will be recorded during June to August (Peat *et al.* 2002).

Testing the effects of competition:

To test the effects of interactions between plants, the performance of the target plants is measured, in relation to the growth and reproductive ability of the plants (i.e. shoot length, number of leaves, etc, depending on the species used). The data collected were quantified using a Relative Neighbour Effect (RNE) index:

$$RNE = (P_{-N} - P_{+N}) / x$$

where P is a measure of plant performance in the presence (+N) and absence (-N) of neighbours, and x is the measure for the species with the greatest performance (Markham & Chanway 1996, Huckle *et al.* 2000). Use of the RNE index makes it possible to quantify both facilitative and competitive interactions without bias, on a scale of +1 to -1, which is standardised, so that pairs of species can be compared. Positive values indicate competition, negative values indicate facilitation and a value of 0 implies that there is no net interaction occurring.

Temperature measurements:

Soil surface temperature were measured in with one of the chambers, shelters and control plots at 5 minute intervals and averaged hourly (Marion *et al.* 1997). Marion (1996) recommends that the temperature be measured at the soil level beneath vegetation cover, to shield the sensors from direct solar radiation. Three sensors were used in the chamber on a north-south transect, with one at the centre and two directly below the top edge of the chamber. One sensor each was used in one of the control units and in one of the shelter units. The temperature were recorded using a Campbell Scientific[®] CR10 datalogger with an AM16 Multiplexer to increase the number of available channels. These measurements were taken in the growing seasons of 2003 and 2004.

2. Seed trapping and seed bank experiment.

Hypothesis: seed from species that are currently rare or absent at higher altitudes is able to move up into the higher areas.

Introduction:

Most high altitude plant species are slow growing, which is an adaptation to the current environmental conditions. One consequence of this slow growth maybe a reduced competitive ability. This could in turn result in a trade-off between competitive ability and survival if the severe abiotic environment is ameliorated by climate change and there is subsequent invasion by plants from lower altitudes.

There is increasing evidence that the global climate is changing. There has been a global temperature rise of about 0.6°C over the last 100 years, with 1998 the single warmest year in the 142 year global instrumental record (Hulme *et al.* 2002). Predictions from the UKCIP 2002 report (Hulme *et al.* 2002) suggest that mean annual temperature in the Scottish Highlands will increase by between 1°C (Low Emissions) and 2°C (High Emissions) over the next 50 years. If climatic change leads to an amelioration of the severity of the abiotic environment at high altitudes, as a result, there is a possibility that some species, which currently do not occur at high altitudes, may be able to establish.

In order to investigate the ability of species to move about the mountain landscape and disperse into areas from which they are currently absent, seed rain will be measured at a number of points along an altitudinal transect. There is much uncertainty as to how climate change will effect seed dispersal and distribution (Watkinson & Gill 2002). Summer temperature has an effect on seed set for many plants (Molau & Larsson 2000, Miller & Cummins 2001), with warmer summers leading to greater seed set. However, current studies suggest that climate change will have little effect on the persistence of seed banks (Akinola *et al.* 1998, Leishman *et al.* 2000). Pakeman *et al.* 1999, have shown that in warmer drier areas of Britain that *Calluna vulgaris* has lower seed bank densities, however they were unable to separate the effect climate has on seed production from seed mortality.

While most seed set by alpine and montane plants is deposited close to the parent (1m radius or less) some can disperse 200-300 m (Molau & Larsson 2000, Pakeman 2001). There is a need for more information on the potential for seed from lower vegetation zones to move to higher levels.

Study area:

This research is being carried out on Glas Tulaichean, Beinn a' Bhuid, Derry Cairngorm and Glas Maol, in the Grampian Mountains of northeast Scotland.

Experimental set up:

Seed trapping:

Seed traps have been put out to see how much seed is arriving at the site and which species are able to move if the conditions are suitable. This experiment

uses seed traps set out at the corners of 2 x 2 m squares. These seed traps consist of 10 cm diameter plastic plant pots with the bottom removed and replaced with 25g/m² frost fleece. The pots are sunk into the ground with the aid of a soil auger and are held in place with pegs on either side, Fig. 1 below. These seed traps are similar to those used by Bullock & Clarke (2000) but with adaptations to make them more suitable for use in the Scottish climate. The advantage of these seed traps is that they are cheap, light to carry yet robust and less visually intrusive than other methods.

Figure 1. Seed trap held in place with two pegs on either side.



At each site, the trapping stations have been established at 50 m height intervals along an altitudinal transect between 700 m and 1,000 m a.s.l. at each site. The location and altitude of the stations have been recorded with a Garmin eTrex Summit GPS receiver and GPS Utility software.

Collection and identification of seed:

The seed traps will be emptied on a monthly basis between June and November 2003, in order to relocate the traps a GPS receiver will be used. The fleece at the bottom of the trap will be removed and placed into a pre marked Ziploc® bag and a fresh clean piece of fleece attached. The traps at each station are numbered clockwise from 1 to 4, with 1 being the trap at the top left corner of the station when facing up hill. The collected fleece will be brought back and examined under magnification (magnifying lens or binocular microscope as required) for seeds. Any seeds found will be removed and identified by comparing with the Macaulay seed collection and counted. The species range of the Macaulay seed collection will be checked against the vegetation survey (see below). If any species expected are found to be missing from the reference collection then reference seed will be collected from the field.

Germination of seed:

In order to test the viability of the seed collected, an attempt will be made to germinate seeds by using the following method. Once identified seed will be placed in plastic petri dishes on to four layers of moistened filter paper. The petri dishes will then be sealed and stored at 4° C in darkness for 6 weeks to break dormancy (Baskin & Baskin 1998, Cummins and Miller 2002, Cummins and Miller 2000, pers com. R. Cummins 2002). Any seed known to require further treatment to break dormancy will be treated in accordance with Cummins and Miller (2000). Up to a maximum 50 pre-treated seeds per species from each trap will then be moved to a greenhouse for incubation, where they will be kept on moistened filter paper (Miller and Cummins 2001). A photoperiod of at least 12 hours in 24 will be maintained with artificial daylight replacement lighting as necessary. Seeds will be recorded as having germinated if the radical projects by more than 1 mm (Miller and Cummins 2001). Incubation will continue until at least 5 weeks after the last seed has germinated.

Seed bank:

The soil cores which were removed when placing the seed traps were taken back to the Macaulay Institute. Once there, they were stored at 1-4° C for a minimum of six weeks and then warmed for four days at 30° C to help break dormancy of the seeds (R. Cummins pers. com.). The cores were then broken up and the soil spread out evenly, to a depth of not more than 1 cm, in individual 21 x 15 cm plastic seed trays lined with capillary matting. The seed trays were then move into a controlled environment growth room, where they were subjected to a 12 hour photo period and a diurnal alternating temperature of 16 / 10° C (12 hours at each temperature) (Cummins pers. com., Baskin & Baskin 1998). The light intensity in the growth room is set to 460-500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ P.A.R. at the level of seed trays. To allow for variations in the growth room the trays were laid in randomised blocks.

The trays are checked on a daily basis to make sure that they are not drying out and observations for seedling emergence are made at intervals of not less than one week. Emerging seedling are allowed to grow on until they could be reliable identified, they are then recorded and removed.

Figure 2. Seed trays in controlled environment growth room.



Vegetation survey:

Seeds produced by most alpine and arctic plants are only dispersed over short distances from the plant, in most cases less than 1 m (Marchand & Roach 1980, McGraw 1980, Spence 1990, Legg *et al.* 1992, Ingersoll & Wilson 1993, Cain *et al.* 2000, Molau & Larsson 2000, Zabinski *et al.* 2000). So a survey of vegetation surrounding each seed trapping station will be carried out to find out which plants are present close to the seed traps.

A survey within a 4 x 4 m quadrat around the seed traps, recording all vascular plants present and their percentage cover was made in July 2003. The quadrats were subdivided into quarters to make the estimates of percentage cover easier, this will be done by taking a line from the permanent central post (place to aid relocation of the trapping station) out to four corner hoops and measuring tape passed round. This dataset will be compared with the seed rain and seedbank datasets, to determine the percentage of seed from local sources.

Acknowledgements:

My thanks to -

Simon & Alex Winton of the Dalmunzie Estate for their assistance and allowing me to use a Landrover to access the site

The Macaulay Development Trust, for supplying the money

And Andrea Britton (Macaulay Institute), Rob Brooker (CEH Banchory) Sarah Woodin (University of Aberdeen).

References:

Aarssen L.W. & Epp G.A. (1990) Neighbour manipulations in natural vegetation: a review. *Journal of Vegetation Science* 1, 30.

Akinola M.O., Thompson K. & Buckland S. M. (1998) Soil Seed Bank of an Upland Calcareous Grassland After 6 Years of Climate and Management Manipulations. *Journal of Applied Ecology* 35, 544-552

Baskin, C.C. & Baskin, J.M. (1998) *Seeds: ecology, biogeography, and evolution of dormancy and germination*. Academic Press, London.

Berry, P.M., Harrison, P. A., Dawson, T. E., & Pearson, R. (2002) Integrated impacts on biodiversity. In: *RegIS: Regional Climate Change Impact Response Studies in East Anglia and North West England*. (Eds. Holman, I.P. & Loveland, P.J.), pp. 192-265. DEFRA, London.

BGS (British Geological Survey) (1989) Braemar, Sheet 65W. 1:50 000 Series. BGS, Edinburgh.

Brooker R.W., Carlsson B.Å. & Callaghan T.V. (2001) *Carex bigelowii* Torrey ex Schweinitz (*C. rigida* Good., non Schrank; *C. hyperborea* Drejer). *Journal of Ecology* 89, 1072-1095.

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

Bullock J.M. & Clarke R.T. (2000) Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia* 124, 506-521.

Cain, M.L., Milligan, B.G. & Strand, A.E. (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany* 87, 1217-1227.

Carlsson B.Å. & Callaghan T.V. (1991) Positive plant interactions in tundra vegetation and the importance of shelter. *Journal of Ecology* 79, 973-989.

Choler P., Michalet, R. & Callaway, R.M. (2001) Facilitation and competition on gradients in Alpine plant communities. *Ecology* 82, 3295-3308.

Cummins R.P. & Miller G.R. (2000) The role of chilling in the germination of some Scottish montane species. *Botanical Journal of Scotland* 52, 171-185.

Cummins R.P. & Miller G.R. (2002) Altitudinal gradients in seed dynamics of *Calluna vulgaris* in eastern Scotland. *Journal of Vegetation Science* 13, 859-866.

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

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

Hollister R.D. & Webber P.J. (2000) Biotic validation of small open-to chambers in a tundra ecosystem. *Global Change Biology* 6, 835-842.

Huckle J.M., Potter J.A. & Marrs R.H. (2000) Influence of environmental factors on the growth and interactions between salt marsh plants: effects of salinity, sediment and waterlogging. *Journal of Ecology* 88, 492-505.

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., & Hill S. (2002) *Climate change scenarios for the United Kingdom: The UKCIP02 scientific report*. Tyndall Centre for Climate Change Research, School of Environmental Science, University of East Anglia, Norwich. 120pp.

Ingersoll C.A. & Wilson M.V. (1993) Buried propagule bank of a high sub-alpine site - microsite variation and comparisons with aboveground vegetation. *Canadian Journal of Botany* 71, 712-717.

IPPC (1994) Climate Change (1994): *Radiative Forcing of Climate Change*. (Houghton J. T., Meira Filho L. G., Bruce J., Lee H., Callander B. A., Haites E., Harris N. & Maskell K. [Eds.]) Cambridge University Press, Cambridge.

- Klanderud K. & Klanderud, K. & Birks, H. J. B. (2003) Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene* 13, 1-6.
- Kershaw K.A. (1960) Cyclic and pattern phenomena as exhibited by *Alchemilla Alpina*. *Journal of Ecology* 48, 443-453.
- Legg C.J., Maltby E. and Proctor M.C.F. (1992) The ecology of severe moorland fire on the North York Moors - seed distribution and seedling establishment of *Calluna vulgaris*. *Journal of Ecology* 80, 737-752.
- Leishman M.R., Masters G. J., Clarke I. P. & Brown V. K. (2000) Seed bank dynamics: the role of fungal pathogens and climate change. *Functional Ecology* 14, 293-299
- Marchand P.J. & Roach D.A. (1980) Reproductive strategies of pioneering alpine species: seed production, dispersal, and germination. *Arctic and Alpine Research* 12, 137-146.
- Markham J.H. & Chanway C.P. (1996) Measuring plant neighbour effects. *Functional Ecology* 10, 548-549.
- Marion G.M. (1996) *Temperature enhancement experiments*. ITEX Manual ITEX Manual (Molau, U. and Mølgaard, P. [Eds.]), pp. 17-22. Danish Polar Center, Copenhagen.
- Marion G.M., Henry G.H.R., Freckman D.W., Johnstone J., Jones G., Jones M.H., Lévesque E., Molau U., Mølgaard P., Parsons A.N., Svoboda J. & Virginia R.A. (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology* 3, 20-32.
- McGraw J.B. (1980) Seed bank size and distribution of seeds on cottongrass tussock tundra, Eagle Creek, Alaska. *Canadian Journal of Botany* 58, 1607-1611.
- Miller G.R. & Cummins R.P. (2001) Geographic variation in seed-setting by heather (*Calluna vulgaris* (L.) Hull) in the Scottish Highlands. *Journal of Biogeography* 28, 1023:1031.
- Morecroft M.D. & Woodward F.I. (1996) Experiments on the causes of altitudinal differences in the leaf nutrient contents, size and δC^{13} of *Alchemilla alpina*. *New Phytologist* 134, 471-479.
- Molau U. & Mølgaard P. (1996) ITEX Manual. Danish Polar Centre, Copenhagen.

Molau U. (1996) *Seed rain monitoring at ITEX sites*. ITEX Manual (Molau, U. & Mølgaard, P. Eds.), p. 42. Danish Polar Center, Copenhagen.

Molau U. & Larsson E.-L. (2000) Seed rain and seed bank along an alpine altitudinal gradient in Swedish Lapland. *Canadian Journal of Botany* 78, 728-747.

Pakeman R.J., Cummins R.P., Miller G.R. & Roy D.B. (1999) Potential climatic control of seedbank density. *Seed Science Research* 9, 101-110.

Pakeman R.J. (2001) Plant migration rates and seed dispersal mechanisms. *Journal of Biogeography* 28, 795-800.

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

Peat H., Fitter A.H., and Ford H. (2002 onward) The Ecological Database of the British Isles, at the University of York.
<http://www.york.ac.uk/res/ecoflora/cfm/ecofl/index.cfm>

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

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

Spence J.R. (1990) Seed rain in grassland, Herbfeld, Snowbank, and Fellfield in the alpine zone, Craigieburn Range, South-Island, New-Zealand. *New Zealand Journal of Botany* 28, 439-450.

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

Watkinson A.R. & Gill J. A. (2002) *Climate change and dispersal*. In: Dispersal Ecology. (Bullock J.M., Kenward R.E., & Hails R.S. [Eds]), pp. 410-428. Blackwell, Oxford.

Watt A.S. & 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.

Zabinski C., Wojtowicz T. & Cole D. (2000) The effects of recreation disturbance on subalpine seed banks in the Rocky Mountains of Montana. *Canadian Journal of Botany* 78, 577-582.

Notes to readers

This project is being carried out under the auspices of The Northern Studies Centre (NSC).

For more information on The Northern Studies Centre go to:
<http://www.mluri.sari.ac.uk/northernstudies/>