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

Abstract:

There is increasing evidence that plants in mountain areas are now being found at higher altitudes than previously. The mechanisms for this are not well understood, so there is a need for more information on the potential for seed to move from lower vegetation zones to higher levels under predicted climate change. In order to investigate the dispersal potential of mountain species, a study was designed to measure seed rain at a number of points along several altitudinal transects in the Grampian Mountains in Scotland, and soil cores were taken to measure the seed bank present. A survey of current vegetation was also carried out at the sites along the altitudinal transects. This showed that as altitude increased, *Calluna* cover decreased and the diversity of other vascular plants increased. The results from the seed trapping do not show sufficient upward seed movement, neither for *Calluna* nor other vascular plants, to support upward migration of lower vegetation zones. The study shows that there is a small *Calluna* seedbank above the vegetation zone where *Calluna* is currently growing. However, it is questionable whether the seedbank would enable *Calluna* to colonise higher altitudes because of high seedling mortality. The size of the *Calluna* seedbanks reported from the 1970's and 1980's is similar to that found by this study.

2.1. Introduction

There is increasing evidence that plants in mountain areas are now being found at higher altitudes than previously. Several studies in Europe have already shown upward migration of plant species, which has been attributed to climate change (Grabherr *et al*. 1994, Grabherr *et al*. 1995, Klanderud & Birks 2003).

Current predictions for future movement of vegetation zones and potential species extinctions (due to arctic/alpine species being forced off the tops of mountains) are based on climate envelope/space approaches (Harrison *et al*. 2001, Berry *et al*. 2002, Woodward & Beerling 1997). A climate envelope may be described as the potential suitable area for a species to grow, based on climatic factors and the current species distributions. This assumes that plant species are occupying all suitable areas, that there is no long distance dispersal (Cain *et al*. 2000), and that species interactions will not change with climatic change (Davis *et al*. 1998a). These modelling assumptions have often not been evaluated by field studies or observations of current distributions and seed dispersal rates (Bullock & Clarke 2000). Because the modelling often relies on sparse data, the results should be interpreted with caution (Davis *et al*. 1998a,b). There is therefore a need to for better understanding of current dispersal rates of mountain plants and how this may affect plant distributions with predicted climatic change (Ellis 2004).

2.1.1. Seed dispersal

There are several ways in which seeds can be dispersed. Askew *et al*. (1997) describe many plants, based on their seed morphology, as either 'wind dispersed' or 'not wind dispersed'. In alpine and arctic plants the main pathway is through dispersal by wind (anemochory). Although dispersal by animals (zoochory) is possible, there is very little literature on zoochory for alpine or arctic plants. Seeds may also be unintentionally dispersed by humans through soil carried on vehicles, movement of topsoil and even the boots of walker, however these mechanisms are unlikely to be common in the uplands (Hodgkinson and Thompson 1997).

There has been a tendency to describe dispersal characteristics of plants based largely on the presence or absence of obvious morphological adaptations. However when Askew *et al*. (1997) developed an electronic measuring system to test this, they found that morphology does not reflect the seeds' true potential for wind dispersal. Berg (1983) and Berg (1988, both cit. in Tollefsrud *et al*. 1998) also showed that the lack of specialised adaptations of the seeds for long distance dispersal need not prevent long distance dispersal by wind.

While most seed set by alpine and montane plants is deposited close to the parent, within 1 m radius or less (Cain *et al*. 2000, Spence 1990, Ingersoll & Wilson 1993, Zabinski *et al*. 2000), some seeds can disperse 200–300 m (Cain *et al.* 2000, Molau & Larsson 2000, Pakeman 2001). Bullock & Clarke (2000) physically measured wind dispersal at a distance of up to 80 m in Dorset with mean cumulative wind speeds not exceeding 400 hour m s^{-1} (their figures). Scotland experiences higher mean cumulative wind speeds than this, which suggests that dispersal distances for similarly sized seeds could be greater in Scotland.

However there is increasing molecular evidence for dispersal over greater distances (up to 300 km, Tollefsrud *et al*. 1998). Tollefsrud *et al*. (1998) used genetic markers and suggested that *Saxifraga cespitosa* (L.) has been able to disperse over distances of 200 km through seed being blown over snow. While genetic studies are useful, they should be treated with caution: Cain *et al*. (2000) pointed out that there is a need to separate gene flow by seed from gene flow by pollen.

Altitudinal limits on seed dispersal can be determined by temperature related effects on seed production (Molau & Larsson 2000, Cummins & Miller 2002) and the distance over which seed can disperse. Seed production at the altitudinal limits of a species may also be affected by earlier flowering phenology, increasing the seed crop, which may lead to increased species diversity and intraspecific genetic diversity of the seed bank (Thórhallsdóttir 1998).

Calluna is currently dominant in the Sub Alpine zone in Scotland (see Section 1.2), and may be one of the species expected to extend its altitudinal range to higher levels with increasing temperatures. In eastern Scotland the current altitudinal range of *Calluna* is 150-960 m a.s.l., with plant cover declining above 600 m (Cummins & Miller 2002). It is known that both altitude and oceanicity have an effect on the setting of *Calluna* seed, the main environmental controls on seed set being mean maximum temperature and total rainfall during August and September (Miller & Cummins 2001).

Seed set in *Calluna* has shown not to be under genetic control (Miller and Cummins 2001), but is dependent mainly on late summer warmth. Altitude is seen to have an effect, in that below 600 m copious viable seed was always set, whereas above 600 m seed-setting could be sparse or in some years fail altogether (Miller & Cummins 1987, 2001). In a study of colonisation of bulldozed tracks in the Cairngorm Mountains, it was found that, while *Calluna* was an important coloniser below 750 m, above this level its success as a coloniser is markedly reduced (Bayfield *et al*. 1984).

Seed set is affected by cool and wet summer weather (Molau & Larsson 2000, Miller & Cummins 2001), which reduces the activity of insect pollinators (Gimingham 1960, Miller & Cummins 1987, Mahy *et al*. 1998), as does high wind speed, which is frequent at higher altitudes (McClatchey 1996). Low temperatures during the flowering period may also hinder the development of the ovule and maturation of seed (Miller & Cummins 2001). Molau and Larsson (2000) found that in Swedish Lapland the cool wet summer of 1995 substantially reduced seed set in all functional groups, particularly in graminoids and herbs. Low temperatures also affect germination rate in *Calluna*, as the seeds do not germinate at temperatures below 10˚ C (Cummins & Miller 2002).

2.1.2. Seed banks

With increasing altitude seed set becomes more prone to failure, but the cold and wet conditions in the soils lead to increasing seed longevity (Miller & Cummins 1987, Miller & Cummins 2001, Thórhallsdóttir 1998, Cummins & Miller 2002, Baskin & Baskin 1998, Thompson 2000, Pakeman *et al*. 1999, Leishman *et al.* 2000). Where the level of seed rain exceeds the level of germination and seed predation, a seed bank can build up in the soil and can form an "ecological memory" over a century or more (Thompson 2000), which can make them a valuable resource for monitoring ecological change. Seeds in seed banks can persist over long time intervals, in some cases up to 200 years (e.g. Molau & Larsson 2000, Miller & Cummins 1987, Cumming & Legg 1995). Estimates for the longevity of *Calluna* in seed banks range from 150 years at 500 m a.s.l. in southern Scotland (Cumming & Legg 1995) to over 200 years above 800 m a.s.l. in the Scottish Highlands (Miller & Cummins 2001, Cummins & Miller 2002).

Not all species present in an area may be represented in the seed bank (Zabinski *et al*. 2000) and seed banks can also have a different composition to surrounding vegetation (Ingersoll & Wilson 1993, Arroyo *et al*. 1999). Most seeds remain ungerminated due to the lack of light cues which trigger germination (Vleeshouwers *et al*. 1995, Thompson 2000). The seeds of many alpine and arctic plants undergo a period of dormancy and need chilling before germination will occur (Cummins & Miller 2000). This dormancy and persistence in seed banks enables populations of plants to continue to exist in areas where seed set can not be relied on in all years (Thompson 2000, Ingersoll & Wilson 1993). This could therefore be a means for plants from lower altitudes to migrate to higher altitudes where they do not currently occur.

Although little is known about the effects of climate change on seed banks, some current studies suggest that climate change will have little effect on the persistence of seed banks (Akinola *et al*. 1998a,b, Leishman *et al*. 2000).

Evidence from experimental warming and cooling of soil seed banks in meadow communities showed no effects (Akinola *et al*. 1998a,b). Pakeman *et al*. (1999) have shown that in warmer drier areas of Britain *Calluna* has lower seed bank densities, however they were unable to separate the effect of climate on seed production from the effect of seed mortality.

2.1.3. Seed trapping

The main problem in determining how far seed can travel from the parent plant is that it is virtually impossible to capture all seeds dispersed from the parent plant. Techniques for investigating plant dispersal include trapping seeds as they are dispersed (e.g. Green & Calogeropoulos 2002, Kollmann & Goetze 1998, Bullock *et al.* 2002, Page *et al.* 2002) or through the use of genetic markers (e.g. Tollefsrud *et al.* 1998).

There is a number of techniques which may be used to trap seeds (Kollmann & Goetze 1998, Page *et al.* 2002). The main types which are appropriate for upland habitats are:

- pitfall trap, where a pot is sunk into the ground with a gauze or fleece bottom to collect the seeds (Bullock & Clarke 2000). Pitfall traps are the cheapest of the trap types listed here, robust, simple to construct and use, low maintenance, however they are open to small mammals which may be seed predators.
- funnel trap (a variation of the pitfall trap), where a funnel is placed into the ground with a collection bag at the bottom (Kollmann & Goetze 1998, Page *et al*. 2002). Funnel traps are easy to construct and use, and are less open to predation from small mammals. Although they normally have a good capture rate, this can be adversely affected by the wind dynamics. They are also more expensive than pitfall traps.
- sticky trap, where a board or dish is painted with a non-drying glue (Marchand & Roach 1980, Kollmann & Goetze 1998, Page *et al*. 2002). Sticky traps have a very high capture rate and prevent predation of seeds by insects, but they also capture dust and insects.

They are high maintenance, and trapping effectiveness may be lost due to rain.

- doormat trap, where a section of Astro Turf™ is fastened to the ground (Molau 1996, Molau & Larsson 2000). Doormat traps are low maintenance and easy to construct, however it is time consuming to collect the seeds, and they are heavy to carry long distances and relatively expensive.
- snow bed trap, where the surface of the snow is skimmed off with a spade from late lying snow beds and seeds are subsequently washed out and collected (Larsson and Molau 2001, Page *et al.* 2002). There is no setup or maintenance cost, and capture rates are better than with artificial techniques. However, reliable snow beds are needed.

Scottish studies of seed dynamics in the uplands have mostly concentrated on *Calluna* (Barclay-Estrup & Gimingham 1975, Barclay-Estrup & Gimingham 1994, Cumming & Legg 1995, Gimingham 1996, Miller & Cummins 1987, Miller & Cummins 2001, Miller & Cummins 2003, Welsh et al. 1990, etc) and few have been above 700m (Bayfield et al. 1984, Cummins & Miller 2002, Miller & Cummins 2003). These have shown that, while *Calluna* produces seeds prolifically and has a long lived seed bank, most seed does not travel more than 1 m from the parent plant. None of the Scottish studies listed above have investigated the potential for movement of vegetation zones due to climate change, but rather looked at recovery after disturbance. They do however provide a record of seedbanks from work mainly carried out during the 1970s and 1980s.

2.1.4. Aims

There is a need for more information on the potential for seed to move from lower vegetation zones to higher levels under predicted climate change. In order to investigate the dispersal limitations of mountain species, seed rain will be measured at a number of points along an altitudinal transect and soil cores taken to measure the seed bank present, to address the following questions:

- 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?

2.2. Methods

2.2.1. Study sites

This work was carried out at four sites in the Grampian Mountains of the Scottish Highlands: Glas Tulaichean, Glas Maol, Beinn a' Bhuird, and Derry Cairngorm (for maps see Figures 2.1a-c, for grid references see Table 2.1). These sites were chosen as they had an appropriate altitudinal range and also have existing paths for access. Access to all sites was agreed with the landowners and, as all sites are designated SSSIs, with Scottish Natural Heritage. The underlying geology of Glas Tulaichean is Caenlochan Schist (BGS 1989a), which is acidic in nature, Beinn a' Bhuird is Biotite granite (BGS 1989a) also acidic, Derry Cairngorm is granite of varying acidity (BGS 1989b), and Glas Maol is more complex, changing from schist to quartzite and back to schist with increasing altitude (BGS 1989a). At two of the sites, Beinn a' Bhuird, and Derry Cairngorm, there is no sheep grazing, at the other two sites, Glas Tulaichean and Glas Maol, where there is some grazing by free ranging sheep. Free ranging deer and mountain hares are present at all sites.

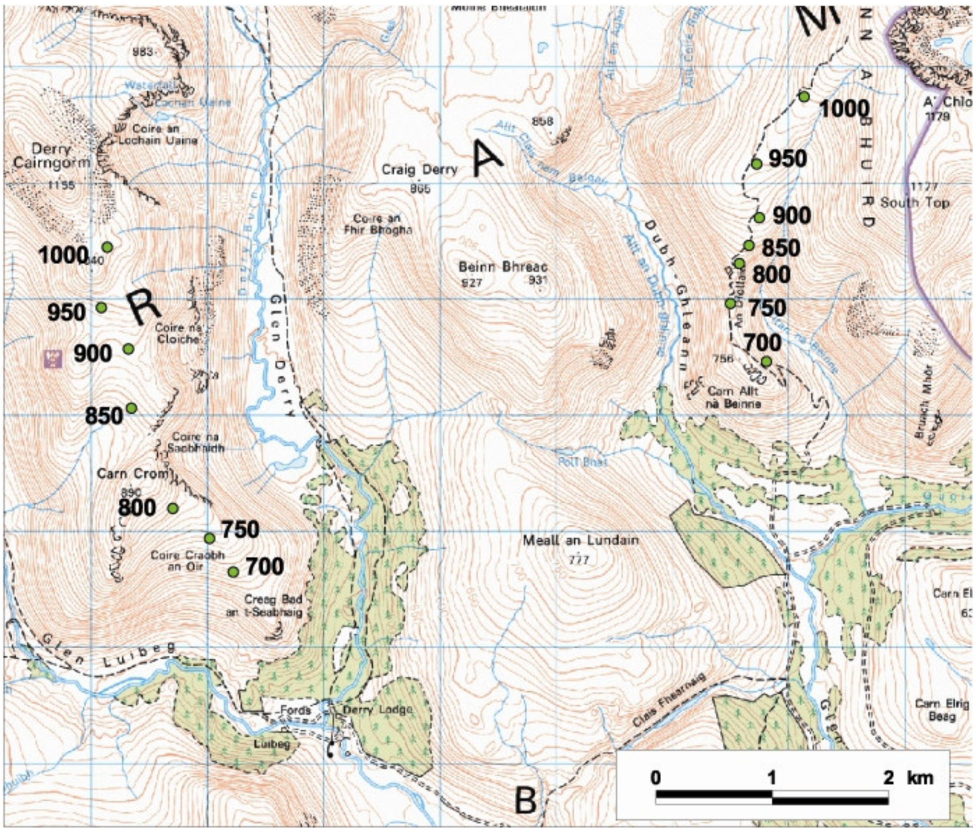

Figure 2.1a. Locations of seed trapping stations on Mar Lodge estate: Derry Cairngorm (left) and Beinn a' Bhuird (right). Stations are numbered according to their altitude in meters above sea level. © Ordnance Survey (with permission). 1:50,000.

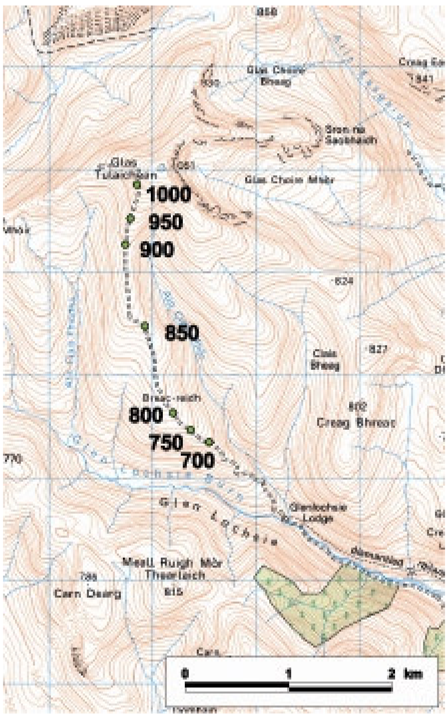

Figure 2.1b. Locations of seed trapping stations on Glas Tulaichean. Stations are numbered according to their altitude in meters above sea level. © Ordnance Survey (with permission). 1:50,000.

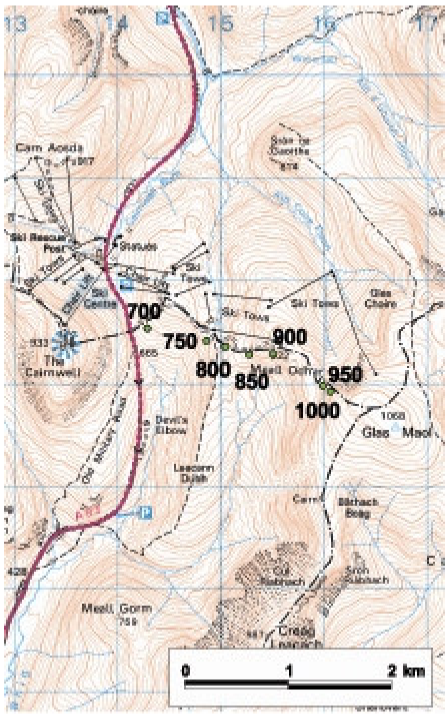

Figure 2.1c. Locations of seed trapping stations on Glas Maol. Stations are numbered according to their altitude in meters above sea level. © Ordnance Survey (with permission). 1:50,000.

Table 2.1. Locations of the seed trapping stations at the four sites (OS grid references in Landranger format).

Altitude above sea level	Glas Tulaichean	Glas Maol	Beinn a' Bhuird	Derry Cairngorm
1,000 m	NO048758	NO160769	NO081987	NO021974
950 m	NO047755	NO159769	NO077981	NO020969
900 m	NO047752	NO155772	NO077976	NO023965
850 m	NO049744	NO152772	NO076974	NO023960
800 m	NO050738	NO150773	NO075973	NO027951
750 m	NO053734	NO148773	NO075969	NO030949
700 m	NO055733	NO142775	NO078964	NO032946

2.2.2. Layout of study

At each station, seed traps were set up to collect seed rain (Section 2.2.4), a vegetation survey was carried out (Section 2.2.3), and soil cores were collected to investigate the existing seed bank (Section 2.2.6). At each site, seed trapping stations were established at 50 m height intervals along an altitudinal gradient between 700 m and 1000 m a.s.l. These were first selected by contour height on an OS map (Landranger Sheet 43, 1:50,000) and for ease of access and location most were sited within 20 m of a path. The grid references of the trapping stations are given in Table 2.1. The latitude, longitude and altitude of the stations were recorded with a GPS receiver (eTrex® Summit, Garmin International Inc) to an accuracy of ± 5m. The altitudinal range was chosen to cover the transition from *Calluna* dominated moorland of the sub alpine habitats to the Scottish arctic/alpine habitats (Figure 1.1).

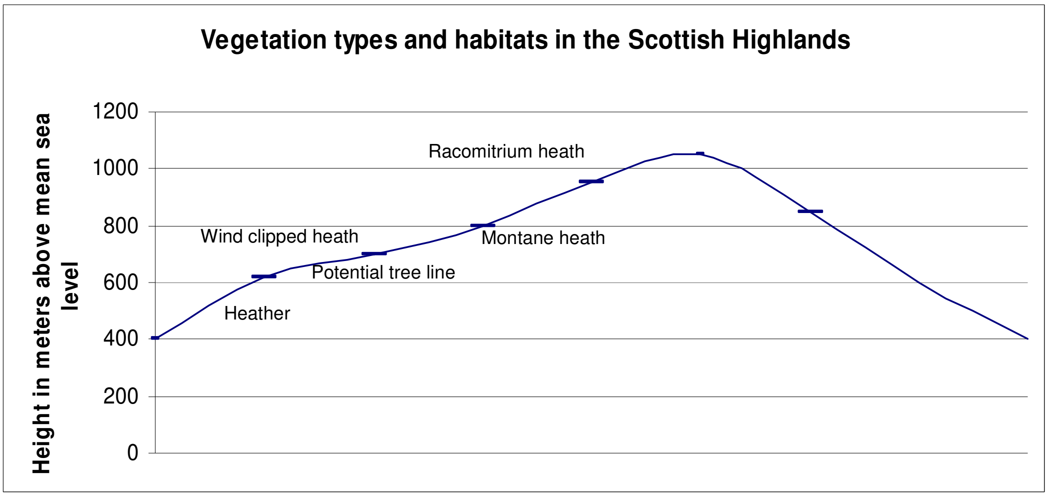

Figure 2.2. A graphical representation of vegetation types and habitats in the Scottish Highlands.

At the Beinn a' Bhuird site no seed was recorded at the 700 m seed trapping station, as it was not possible to relocate the seed traps after the initial visit. The landowner, National Trust for Scotland, had insisted on only short posts being used to mark sites, and at this trapping station the *Calluna* was much taller than the post. Consequently no seed data are available, and the vegetation survey represents the only estimate of the species there. A list of species was recorded in the area of the GPS coordinates, i.e. somewhere within 10 m of the trapping station.

2.2.3. Vegetation surveys

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 the vegetation surrounding each seed trapping station was carried out to determine which plants were present close to the seed traps.

A 4 m by 4 m quadrat around the seed trapping station was surveyed (see Figure 2.3). A record of all vascular plants present and an estimate by eye of the percentage cover of each species were made. Subdividing the quadrat into quarters aided the estimates of percentage cover. This was be done by placing a post with four 2.83 m lines attached next to the permanent central post (placed to aid relocation of the trapping station). The lines were run out at the four points of the compass and pegged down with a wire hoop, and a tape measures was then run round to form the outer perimeter of the quadrat. Using a tape measure also has the advantage that quick and easy checks can be made to ensure that the area of the quadrat remains consistent.

The vegetation survey at all sites was carried out between 23rd June and 6th August 2003, the plant nomenclature follows Stace (1997). This dataset was then used together with the seed rain and seedbank datasets, to determine if the seed was likely to be from local sources.

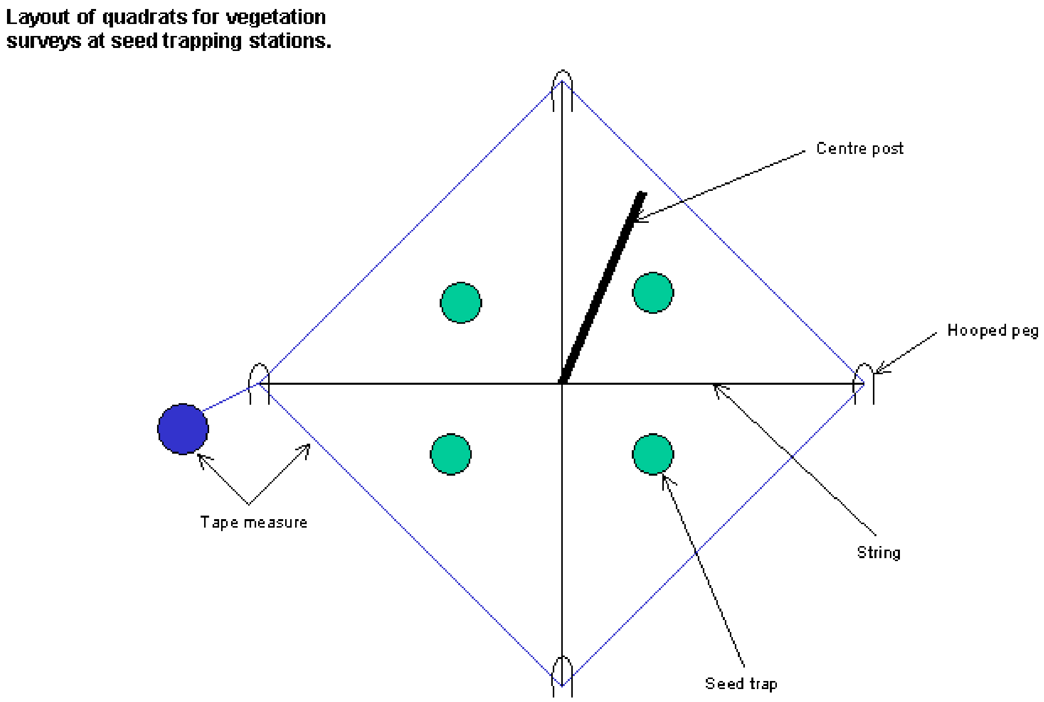

Figure 2.3. Layout of 4 x 4 m quadrat used for the vegetation survey of the seed trapping stations. This technique uses a post with four 2.83 m lengths of string attached, each with a wire hooped peg at the end. This post is then placed the centre of the quadrat, the strings are pegged out at the four points of the compass and a tape measure run round to form the out perimeter of the quadrat. This provides a quick and easy way of establishing a consistently sized quadrat, also the quartering of the quadrat aids estimates of percentage cover made by eye.

2.2.4. Seed trapping

Seed traps were laid out to investigate how much seed was arriving at these sites and which, if any, species of plant would be able to move to these sites and grow if the conditions were suitable. This study used pitfall type seed traps set out at the corners of 2 x 2 m squares (Figure 2.3). The middle of the squares was marked with short wooden post as a visible marker to aid relocation. The seed traps were similar to those used by Bullock & Clarke (2000), and consist of plastic plant pots with a diameter of 10 cm, with the bottoms removed and replaced with 25g/m^2 frost fleece. These pots were then sunk into the ground with the aid of a soil auger and held in place with two pegs on either side (see Figure 2.4). The advantage of these seed traps is that they are cheap, light to carry yet robust and less visually intrusive than other methods, e.g. the ITEX door mat technique (see Section 2.1.3).

The seed traps were laid out between November and December 2002. The content of the seed traps was collected on a monthly basis between April and November 2003, and May and August 2004 (the start of collection was delayed in 2004 by late snow). At these collections the fleece at the bottom of each trap was removed and placed into an individually labelled zip lock bag, which was then sealed for transport and storage. A new square of fleece was then attached to the trap and the trap replaced. Samples of any beetles found in the traps were also taken back to the Macaulay Institute for identification. It was established that none were seed eaters.

Figure 2.4. Pitfall seed trap sunk into the ground and held in place with two pegs, one on either side.

2.2.5. Seed identification

The fleeces collected from the seed traps were brought back to the Macaulay Institute, where necessary dried in the drying room at 30℃, and then examined under a low powered microscope. Any seeds found were removed and compared with the Macaulay seed collection for identification. All seeds where then stored in labelled Petri dishes. These were then taken to the Royal Botanic Gardens Edinburgh (RGBE) for identification of seeds which were not available in the Macaulay collection. Seed which had been previously identified was also checked. At RGBE the seeds where keyed out using Swarbrick (1969) and compared with herbarium specimens from the Scottish collection.

2.2.6. Seed bank

When the seed traps were put in place, soil cores were collected using a 10 cm diameter soil auger, coring to the depth of the seed traps (Pakeman *et al.* 1999), where the soil depth permitted. At a few points rocks prevented this.

Each core was cut to a depth of 5 cm and placed into a separate zip lock bag which was sealed for transport and storage. The cores were taken back to the Macaulay Institute for use in the seed bank study.

The cores were stored in the dark at 4℃ for a minimum of six weeks and then dried at 30℃ for four days, to break dormancy of the seeds (R. Cummins pers. comm.). 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 moved into a controlled environment growth room, where they were exposed to a 12 hour photo period and a diurnal temperature cycle of 16 / 10℃ (12 hours at each temperature) (Cummins pers. comm., Baskin & Baskin 1998). The light intensity in the growth room was set to 460-500 µmol m^{-2} s^{-1} P.A.R. at the level of the seed trays. To allow for environmental variations in the growth room, the trays were laid out in four blocks (see Figure 2.5.) and the position of the trays within the blocks randomised. After six months the position of the trays within each block was changed to a new randomly selected position.

The trays were checked on a daily basis and watered as needed to ensure that they were not drying out. Observations of seedling emergence were made at intervals of no less than one week. Emerging seedlings were allowed to grow on until they could be reliably identified. They were then recorded and removed. Some seedlings such as *Calluna* could easily be identified by their red stem and leaf shape, and were removed straight away (see Figures 2.6 and 2.7). Some seedlings, such as the *Carex* sp. seedling shown in Figure 2.8, could not be so easily identified and needed to be re-potted, tagged and moved to a greenhouse, where they were allowed to grow on until reliable identification could be made.

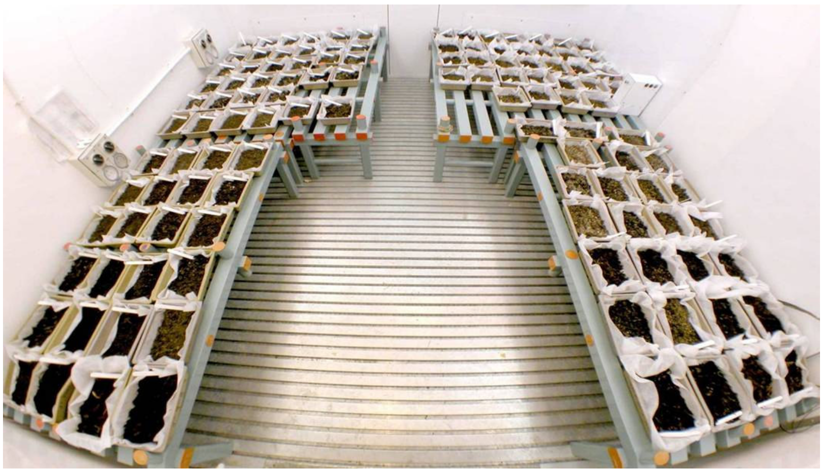

Figure 2.5. Trays containing the soil cores collected for the seedbank trial, laid out in four blocks in the growth room. The positions of the trays within each block were assigned at random.

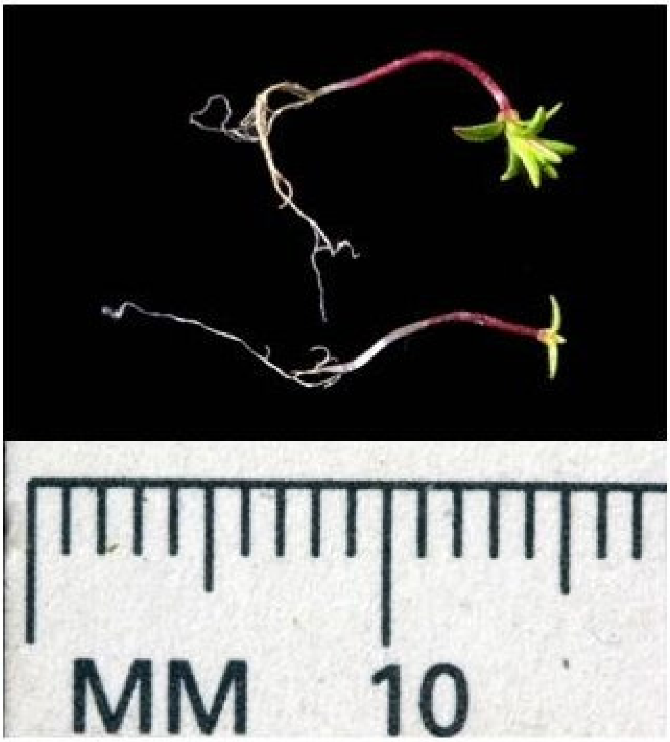

Figure 2.6. *Calluna* seedlings after being removed from a seed tray for counting, the red stem and leaf shape are easily recognised characteristics.

Figure 2.7. Seed tray containing a soil core from Beinn a' Bhuird, showing *Calluna* seedlings which were removed, counted and recorded.

Figure 2.8. *Carex* seedling in seed tray which needs to be re-potted and moved to greenhouse in order for it to grow large enough to be reliably identified.

2.2.7. Statistical Analysis and Data Handling

The diversity of vascular plants at each station was described using a Simpson's diversity index (1-*D*) and a Simpson's measure of evenness (E_{1-D}). Smith and Wilson (1996) define evenness as equal abundance of species in a community, i.e. a community where each species present is equally abundant has high evenness, a community with large differences in species abundance has low evenness. As the sample size was small, Simpson's index is appropriate as it a robust and meaningful measure of diversity (Magurran 2004). In order to determine if the changes in diversity and evenness were significant, a two way analysis of variance (ANOVA) was used.

Statistical analysis was then carried out to examine if there was a change in the relationship between the percent of plants in the surface vegetation which are represented in the seed rain with altitude. An angular transformation before regression was used to test if the changes with altitude were significant. To check if the interannual variation in *Calluna* seed rain between the two years of the study was significant, the data were log-transformed and a paired t-test was used.

Data from the *Calluna* seedbank and current seed rain was plotted on a log scale for ease of visual interpretation. An estimate of the seedbank and current seed rain per square metre was made to enable comparisons with data from other published studies.

2.3. Results

2.3.1. Vegetation survey

At the lower end of the transects, between 700 and 850 m in the sub alpine zone (see Chapter 1), *Calluna* was the dominant vascular plant species at all four sites (Table 2.2). Above 800 m the vegetation is increasingly wind clipped and prostrate. At most sites below 850 m the *Calluna* was observed to be in the building phase, that is the *Calluna* has a closed canopy and is actively growing (Gimingham 1960, 1996). The exception to this was at the 700 m trapping station on Glas Maol, where the *Calluna* was observed to be in the degenerative phase, i.e. where the canopy is breaking up (Gimingham

1960, 1996). The highest *Calluna* cover was found on Beinn a' Bhuird and Derry Cairngorm, where it reached 950 m. On Glas Maol *Calluna* was not recorded above 850 m.

Table 2.2. Estimated percentage *Calluna* cover recorded at each seed trapping station.

Altitude	Beinn a' Bhuird	Derry Cairngorm	Glas Maol	Glas Tulaichean
700m	100 %	85 %	50 %	100 %
750m	95 %	60 %	85 %	100 %
800m	80 %	90 %	50 %	85 %
850m	45 %	93 %	75 %	83 %
900m	84 %	5 %	0	57 %
950m	15 %	10 %	0	0
1000m	0	0	0	0

Above 850 m there was an increase in species diversity at all sites, where no one species of vascular plant was dominant. One *Pinus sylvestris* seedling was recorded at 750 m on Derry Cairngorm, unfortunately it was too small to age by non destructive techniques. A full list of all species recorded for the vegetation survey is given in Appendix 1.

A measure of the diversity of vascular plant species was calculated using Simpson's diversity index and Simpson's measure of evenness (E_{1-D}) at each trapping station (Magurran 2004). As Simpson's diversity index tends to reflect dominance, the evenness was also calculated to determine whether the sample was skewed by the presence of one or more dominant species. The results are shown in Table 2.3. Levels of diversity generally increased with altitude, while evenness decreased at all sites. Glas Maol showed the highest levels of diversity and also the most evenness.

Table 2.3a. The diversity and evenness of vascular plant species found at 50m altitudinal intervals at all four sites shown using a Simpson's diversity index (1-*D*) and Simpson's measure of evenness (E_{1-D}).

Diversity	Beinn a' Bhuird	Derry Cairngorm	Glas Maol	Glas Tulaichean
700m	0.125	0.158	0.682	0.086
750m	0.109	0.34	0.286	0.054
800m	0.198	0.134	0.561	0.262
850m	0.586	0.096	0.367	0.282
900m	0.193	0.66	0.673	0.523
950m	0.72	0.56	0.817	0.801
1000m	0.496	0.733	0.872	0.764
Evenness				
700m	1.994	1.268	0.049	1.928
750m	1.313	0.979	0.317	4.629
800m	0.562	1.864	0.223	0.545

850m	0.213	1.732	0.227	0.443
900m	0.739	0.189	0.186	0.239
950m	0.198	0.099	0.094	0.096
1000m	0.224	0.105	0.088	0.145

Table 2.3b. An analysis of the effects of altitude on diversity and evenness, showing the results of the ANOVA are given below. Significant values are given in bold.

Diversity	d.f.	s.s.	P value
Altitude	6	1.148	**<0.001**
Site	3	0.294	**0.035**
Evenness			
Altitude	6	9.53	0.099
Site	3	3.59	0.221

2.3.2. Seed trapping

All seeds collected in the seed traps were identified to genus and where possible to species and the results summarized over both years (Table 2.4). As with the seedlings emerging from the seedbank, most of the seeds collected in the seed traps at lower levels were *Calluna*, with the exception of Glas Maol, where other species were dominant at some stations. On Beinn a' Bhuird and Derry Cairngorm at higher levels (above 850 m) *Juncus trifidus* was the most commonly recorded seed. Most of the seeds collected were from species which were recorded at the same trapping station in the vegetation survey. There were some seeds collected from the seed traps which were recorded at the site but not a that individual trapping station. These are highlighted in green in Table 2.4. Where the seeds are from species which were not recorded in the vegetation survey at the site, they are highlighted in yellow.

Table 2.4. Seeds collected in the seed traps between November/December 2002 and August 2004 at the trapping stations along altitudinal transects at the fours different sites. The numbers in brackets show *Calluna* seed as a percentage of the total of the seeds trapped at this site. Numbers highlighted in green are recorded at the site but not the individual trapping station and numbers highlighted in yellow are species not recorded at that site.

Altitude and site	*Betula nana*	*Calluna vulgaris*	*Carex bigelowii*	*Carex pilulifera*	*Cirsium* sp.	*Deschampsia cespitosa*	*Deschampsia flexuosa*	*Empetrum nigrum*	*Erica tetralix*	*Festuca ovina*	*Festuca vivipara*	*Galium saxatile*	*Gnaphalium supinum*	*Juncus acutiflorus*	*Juncus squarrosus*	*Juncus trifidus*	*Nardus stricta*	*Potentilla erecta*	*Trichophorum cespitosum*
Beinn a' Bhuird																			
700 m*																			
750 m		239 (100)																	
800 m		34 (97.1)						1											
850 m		7 (31.8)												1		14			
900 m																25			
950 m																31			
1000 m																46			
Derry Cairngorm																			
700 m		204 (100)																	
750 m		88 (100)																	
800 m		85 (78)		24															
850 m		109 (96.5)		4															
900 m									1							3			
950 m				4			4									7		2	4
1000 m																38			

* N.B. The seed trapping station was missing (see Section 2.2.2).

Altitude and site	*Betula nana*	*Calluna vulgaris*	*Carex bigelowii*	*Carex pilulifera*	*Cirsium* sp.	*Deschampsia cespitosa*	*Deschampsia flexuosa*	*Empetrum nigrum*	*Erica tetralix*	*Festuca ovina*	*Festuca vivipara*	*Galium saxatile*	*Gnaphalium supinum*	*Juncus acutiflorus*	*Juncus squarrosus*	*Juncus trifidus*	*Nardus stricta*	*Potentilla erecta*	*Trichophorum cespitosum*
Glas Maol																			
700 m		19 (73.1)					2			1				3			1		
750 m		9 (42.9)													12				
800 m		6 (85.7)															1		
850 m		4 (20)		8					1			6					1		
900 m					2	3				1							1		
950 m			1				19				2								
1000 m										2		10	11						
Glas Tulaichean																			
700 m		125 (99.2)								1									
750 m		50 (98)								1									
800 m	1	14 (93.3)																	
850 m		42 (100)																	
900 m																			
950 m										3						2			
1000 m							1									1			

Again as with the seedlings, for most of the species present in the surface vegetation no seed was recorded (Table 2.5). Overall there is high variability between stations, with 0 - 40% of the number of species present in the seedbank (as % of species in the surface vegetation). No clear patterns related to altitude were found, a regression showed there were no significant differences. However, Beinn a' Bhuird shows slightly lower mean percentage values than the other sites.

Table 2.5. Percentage of vascular plant species present in the surface vegetation which are represented in the seed rain from both years at all four sites. The results of the regression analysis (change with altitude) are given below.

Altitude	Beinn a' Bhuird	Derry Cairngorm	Glas Maol	Glas Tulaichean
700 m	n/a	14 %	12 %	29 %
750 m	13 %	17 %	18 %	40 %
800 m	8 %	33 %	18 %	10 %
850 m	10 %	22 %	27 %	8 %
900 m	11 %	8 %	22 %	0 %
950 m	13 %	20 %	20 %	13 %
1000 m	8 %	7 %	19 %	18 %
mean	10 %	17 %	19 %	17 %

Site	d.f.	s.s.	P value
Beinn a' Bhuird	1,4	10.3	0.69
Derry Cairngorm	1,5	41.5	0.40
Glas Maol	1,5	18.1	0.23
Glas Tulaichean	1,5	212.1	0.28

2.3.3. Seed bank

Seedlings germinated from the seed bank were identified to genus and where possible species (Table 2.6). The most common species of seedling to germinate from the seed bank was *Calluna*, and this was found at its highest density below 850m. With the exception of Glas Maol, *Calluna* seedlings continued to be the most common seedlings emerging from the seedbank above the level where *Calluna* cover was not dominant (Table 2.6). Above 900m, *Calluna* seedlings emerged from the seedbank even though no *Calluna* cover was recorded at the trapping stations at all sites, with the exception of Glas Maol, where no seedlings emerged from the seedbank above 850m (Table 2.6).

After *Calluna*, *C. bigelowii* was the most commonly recorded seedling to emerge from the seedbank at all sites. The exception to this was on Glas

Maol where *G. saxatile* was slightly more common (Table 2.6). An estimate of the density of the seedbank for *C. bigelowii* was made by multiplying the number of seedlings recorded by the area of the soil cores at each trapping station. Estimated seedbank densities for *C. bigelowii* are given Table 2.8. However only one seed was recorded in the seed traps, at 950 m on Glas Tulaichean.

Most of the seedlings recorded emerging from the seedbank were of species found in the vegetation survey at seed trapping stations where the soil cores were collected (Table 2.6). However some seedlings germinated from the seedbank at sites (transects) where that species had not been recorded in the vegetation survey for the individual trapping station (highlighted in green in Table 2.6). Other seedlings were also recorded emerging from the seedbank, but were not recorded anywhere at that site (transect) in the vegetation survey, these are highlighted in yellow in Table 2.6. However the majority of vascular plant species which were recorded in the vegetation survey were not represented in the seedbank (Table 2.8).

Table 2.6. Seedlings germinated from soil cores collected along altitudinal transects at the four different sites. The numbers in brackets show *Calluna* seedlings as a percentage of the total seedling emergence from the seedbank at that station. Numbers highlighted in green are species recorded at the site in the vegetation survey but not at the individual trapping station. Numbers highlighted in yellow are species found in the seedbank but not recorded in the vegetation survey anywhere at that site.

Site / Altitude	*Agrostis* Sp.	*Anthoxanthum odoratum*	*Calluna vulgaris*	*Carex bigelowii*	*Empetrum nigrum*	*Festuca ovina / vivipara*	*Galium saxatile*	*Juncus squarrosus*	*Juncus trifidus*	*Luzula multiflora*	*Nardus stricta*	*Poa annua*	*Potentilla erecta*	*Sagina* Sp.	*Vaccinium myrtillus*
Beinn a' Bhuird															
700 m			666 (99.9)									1			
750 m			440 (100)												
800 m			368 (95.1)	17					2						
850 m		1	126 (86.9)	17											1
900 m			76 (97.4)	2											
950 m				1					4						
1000 m			1 (20)						4						
Derry Cairngorm															
700 m			363 (98.1)	5						2					
750 m			254 (98.8)	1						2					
800 m			242 (94.2)	15											
850 m			579 (99.5)	2							1				
900 m			5 (100)												
950 m			9 (75)		2				1						
1000 m			2 (50)						2						
Glas Maol															
700 m	4		228 (92.7)	2		2	4	1			2		1	2	
750 m			2072 (99.9)					1						1	
800 m			375 (99.5)	1									1		
850 m			199 (100)												
900 m	1			1			3			1					
950 m				1			1			1					
1000 m															
Glas Tulaichean															
700 m			142 (100)												
750 m			165 (99.4)							1					
800 m			301 (100)												
850 m			489 (99.8)						1						
900 m			33 (94.3)	2											
950 m			2 (33.3)	2					2						
1000 m			4 (50)	2					2						

Table 2.7. Estimated seedbank densities for *C. bigelowii* (seedlings per m^2) at the four sites.

Altitude	Beinn a' Bhuird	Derry Cairngorm	Glas Maol	Glas Tulaichean
700 m		135	54	
750 m		27		
800 m	459	405	27	
850 m	459	54		
900 m	54		27	54
950 m	27		27	54
1000 m				54

Table 2.8. Percentage of vascular plant species present in the surface vegetation which are represented in the seedbank, by seedling emergence, at all four sites. The results of the regression analysis of change with altitude are given below.

Altitude	Beinn a' Bhuird	Derry Cairngorm	Glas Maol	Glas Tulaichean
700 m	25 %	29 %	21 %	14 %
750 m	13 %	33 %	18 %	20 %
800 m	17 %	33 %	27 %	10 %
850 m	40 %	33 %	7 %	8 %
900 m	22 %	0 %	33 %	20 %
950 m	25 %	5 %	13 %	13 %
1000 m	8 %	0 %	0 %	18 %
mean	21 %	19 %	17 %	15 %

Site	d.f.	s.s.	P value
Beinn a' Bhuird	1,5	13.4	0.66
Derry Cairngorm	1,5	112	0.24
Glas Maol	1,5	225.7	0.22
Glas Tulaichean	1,5	1.59	0.78

2.3.4. Analysis relating current seed rain (seed trapping) to historic seed rain (seed bank)

Non Calluna species

Data on the occurrence of plant species at the four sites were compared to determine if there was seed arriving at the sites from plants not currently present there. Due to the low numbers of non *Calluna* seeds collected, no formal statistical analysis was carried out. Only a few species not recorded in the vegetation survey of the site were found either in the seed traps or the seedbank. These are shown in Table 2.9 below. Species for which either seeds or seedlings were found with no cover at that trapping station are shown in Table 2.10.

Table 2.9. Plant species which were not recorded in the vegetation survey for the site but were recorded in either the seed traps or the seedbank. The number of seeds or seedlings is shown in brackets after the species name.

Site	Altitude	From seed trap	From seedbank
Beinn a' Bhuird	700 m*		*Poa annua* (1)
	850 m	*Juncus acutiflorus* (1)	
	850 m		*Anthoxanthum odoratum* (1)
Derry Cairngorm	700 m		*Luzula multiflora* (2)
	750 m		*Luzula multiflora* (2)
Glas Maol	700 m	*Juncus acutiflorus* (3)	
	700 m		*Potentilla erecta* (1)
	700 m		*Sagina procumbens* (2)
	750 m		*Sagina procumbens* (1)
	800 m		*Potentilla erecta* (1)
	850 m	*Erica tetralix* (1)	
	900 m	*Cirsium* sp. (2)	
Glas Tulaichean	750 m		*Luzula multiflora* (1)
	800 m	*Betula nana* (1)	

* N.B. The seed trapping station was missing (see Section 2.2.2).

The numbers of species (either as seeds and seedlings) not found in the vegetation survey at all (Table 2.9) were smaller than the number of species recorded at the site but not at the trapping station (Table 2.10). Most of the species found are common and would be expected to be present in these habitats. The one rare species found was a single *Betula nana* seed at 800 m on Glas Tulaichean, the nearest known site is more than 11 km away near Bynack Lodge (Dundee Museum's Local Record Centre, pers. comm.).

Table 2.10. Plant species which were recorded in the vegetation survey for the site (transect) but not at the individual seed trapping station where they were recorded in either the seed traps or the seedbank. The number of seeds or seedlings is shown in brackets after the species name.

Site	Altitude	From seed trap	From seedbank
Beinn a' Bhuird	800 m	*Empetrum nigrum* (1)	*Carex bigelowii* (17)
	850 m	*Juncus trifidus* (14)	
	1000 m	*Calluna vulgaris* (1)	
Derry Cairngorm	700 m		*Carex bigelowii* (5)
	750 m		*Carex bigelowii* (1)
	900 m	*Erica tetralix* (1)	*Calluna vulgaris* (5)
	950 m	*Carex pilulifera* (4)	*Calluna vulgaris* (9)
	950 m	*Juncus trifidus* (7)	*Juncus trifidus* (1)
	1000 m	*Juncus trifidus* (38)	*Calluna vulgaris* (2)
	1000 m		*Juncus trifidus* (2)
Glas Maol	700m		*Carex bigelowii* (1)
	900m	*Festuca ovina / vivipara* (1)	*Luzula multiflora* (1)
	950 m		*Luzula multiflora* (1)
Glas Tulaichean	850 m		*Juncus trifidus* (1)
	950 m		*Calluna vulgaris* (2)
	1000 m		*Calluna vulgaris* (4)

Calluna

At all sites the emergence of *Calluna* seedlings from the seed bank was greater than the current seed rain. At most of the sites seedlings were observed emerging from the seedbank at higher altitudes than seed was collected (Figures 2.9 and 2.10). The highest recorded *Calluna* seed was at 900m on Beinn a' Bhuird, at the other sites *Calluna* seed was not found above 850m (Figures 2.9 and 2.10, and Table 2.4). The highest altitude where *Calluna* was recorded growing was 950m on Derry Cairngorm, at none of sites *Calluna* plants were recorded growing at the 1000m station (Table 2.2). At three sites, Beinn a' Bhuird, Derry Cairngorm and Glas Tulaichean, *Calluna* seedlings were emerging from the seedbank at altitudes above the highest recorded *Calluna* seed (Table 2.6). At the same sites *Calluna* seedlings were also observed to emerge from the seedbank of trapping stations where *Calluna* plants are currently absent.

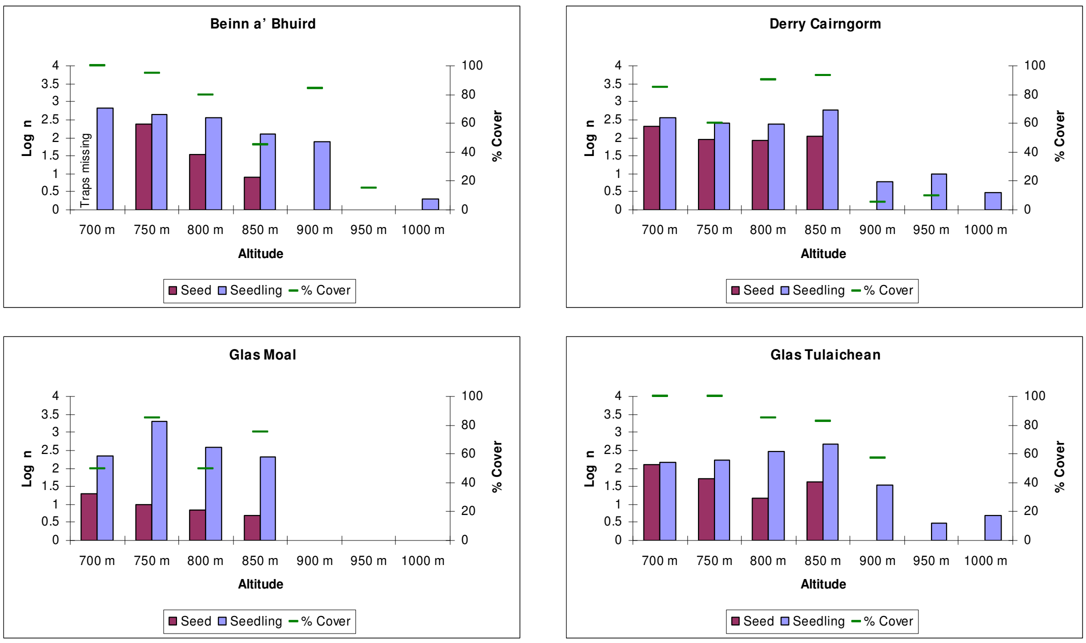

Figure 2.9. Number of Calluna seeds collected (during both years) and seedlings emerging from the seedbank in comparison with percentage cover at different altitudes. Seed and seedling numbers are given on a log scale to make visual comparison easier.

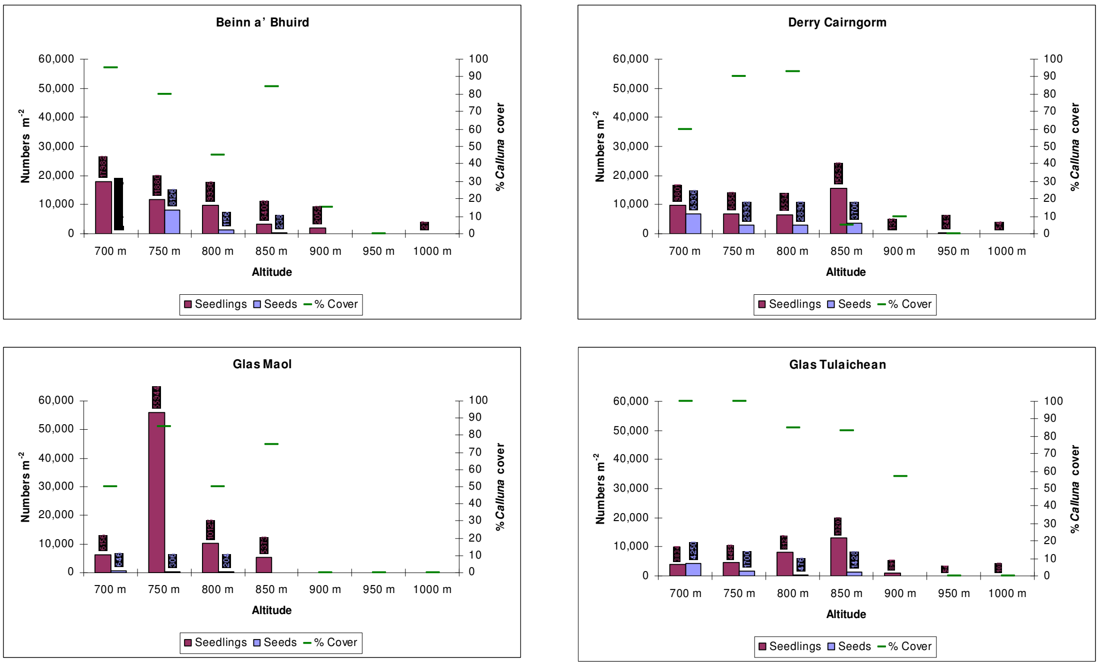

Figure 2.10 Density (n m^{-2}) of *Calluna* seed and seedlings at each altitude at all four sites for both years.

The analysis so far has used the total seed rain over the two years during which data were collected (November/December 2002 until August 2004), to average out differences in interannual variation for comparison with the seedbank. Table 2.11. shows the interannual variation for *Calluna* between the two years for which seeds were collected. At higher altitudes *Calluna* seed dispersal occurs between December and June (Cummins and Miller 2002), therefore the seed rain collected during 2003 and 2004 represents the seed production during two full years, i.e. 2002 and 2003. There is considerable variation between the two years at most seed trapping stations, with greater seed capture during 2004. This difference is shown to be significant.

Table 2.11 Interannual variation in *Calluna* seed rain at the four sites, collected during 2003 and 2004, representing seed production during 2002 and 2003. The results of the paired t-test are shown below and significant values are given in bold.

Altitude	Site Name	Seed count 2003	Seed count 2004	2003 (as % of total)	2004 (as % of total)
750 m	Beinn a' Bhuird	119	120	50%	50%
800 m	Beinn a' Bhuird	8	26	24%	76%
850 m	Beinn a' Bhuird	2	5	29%	71%
700 m	Derry Cairngorm	77	127	38%	62%
750 m	Derry Cairngorm	49	39	56%	44%
800 m	Derry Cairngorm	52	33	61%	39%
850 m	Derry Cairngorm	25	84	23%	77%
700 m	Glas Maol	0	18	0%	100%
750 m	Glas Maol	0	9	0%	100%
800 m	Glas Maol	4	0	100%	0%
850 m	Glas Maol	4	0	100%	0%
700 m	Glas Tulaichean	26	99	21%	79%
750 m	Glas Tulaichean	7	43	14%	86%
800 m	Glas Tulaichean	5	13	28%	72%
850 m	Glas Tulaichean	0	38	0%	100%
Sum	Beinn a' Bhuird	129	151	46%	54%
Sum	Derry Cairngorm	203	283	42%	58%
Sum	Glas Maol	8	27	23%	77%
Sum	Glas Tulaichean	38	193	16%	84%
Sum	All Sites	378	654	37%	63%

Results of paired t-test	Mean	Variance	Standard deviation	Standard error of mean	P value
	-0.8244	2.236	1.495	0.3861	**0.051**

2.4. Discussion

2.4.1. Potential for plants to move – upward shift in vegetation?

This study investigated the potential for plants to move by comparing the surface vegetation with current seed rain and seedbank. If there is upward movement, different species are likely to move at different rates (Gottfried *et al*. 1999). The strongest signal in the data was for *Calluna* which is discussed in greater detail below. For other species there was insufficient data available to allow firm conclusions to be drawn. Possible factors influencing the migration of plants under predicted climate change, influences other than climate change as well as uncertainties are also discussed.

Calluna

The majority of seedlings emerging from the seedbank were *Calluna*, irrespective of altitude (Section 2.3.3). This is similar to the results reported by Miller and Cummins (2003). As with seedlings from the seedbank, *Calluna* seeds were very common at lower levels, however no *Calluna* seed was recorded in the seed traps above 850 m.

Most studies of *Calluna* seed dispersal and seedbanks are from lowland heaths. There are only few relevant studies from the Highlands and these were carried out by G. Miller and R. Cummins 20 to 30 years before the present study in the Grampian mountains (e.g. Miller & Cummins 1987, Cummins & Miller 2002). As no details were available for the exact location of the sites they used, it was not possible to make a direct comparison between their data and data from this study. Some general comparisons can be made though.

In this study the numbers of germinable *Calluna* seeds m^{-2} in the seedbank between 800 and 900 m a.s.l. was >9,500. In comparison, Miller and Cummins (1987) and Cummins and Miller (2002) report > 10,000 germinable *Calluna* seeds m^{-2} in the seedbank between 800 and 900 m a.s.l. It should be noted that both studies used similar methods for soil collection and germination, also the same length of time was allowed for germination. In contrast this study found a mean annual seed deposition of 550 m^{-2} above 800 m a.s.l., which is considerably lower than the 900 seeds m^{-2} reported by Cummins and Miller (2002).

While there was no *Calluna* seed found in the current seed rain above 850m at any of the sites, in spite of the favourable conditions for seed set in the summer of 2003, there were germinable seeds in the seed banks above 850m at all sites with one exception. On Glas Maol, there is no *Calluna* seedling emergence above 850 m, which would suggest that *Calluna* has been absent from the area where the trapping stations were located for a considerable period of time, given that *Calluna* seeds can survive in the seed bank for more the 150 years (Cumming & Legg 1995, Miller & Cummins 2001, Cummins & Miller 2002). The seedling emergence from the seed bank continued above the altitude with *Calluna* in the surface vegetation at the trapping stations, which stopped at 950 m on Derry Cairngorm and Beinn a' Bhuird[1], and 900 m on Glas Tulaichean.

There are two possible scenarios which may explain the occurrence of *Calluna* seeds in the seedbank beyond the level of current *Calluna* surface cover at the trapping stations, and well beyond the currently recorded seed rain:

Firstly, the seeds in the seedbank could represent an upward shift of *Calluna*, with vagrant seeds arriving from lower levels being incorporated into the seedbank, but currently unable to germinate due to low soil temperatures. Given that most Calluna seeds are deposited within 1 m of the parent plant (Bullock & Clarke 2000, Legg *et al*. 1992, Gimingham 1960), and the observed seed rain and *Calluna* seed set being unreliable in many years at altitudes above 600 m (Miller and Cummins 2001), soil seed banks may represent recruitment from only a few years or even just one crop of seeds (Thórhallsdóttir 1998).

Secondly, the seedbanks may be remnants of former populations of *Calluna* at these sites. Given that these seedbanks are very long lived, the seeds found in the seedbanks could be the last remaining seeds of formerly more extensive *Calluna* cover. A possible mechanism for this would be endozoochory, as *Calluna* seeds can survive passage through the gut of grazing animals (Welsh 1985, Welsh *et al*. 1990, Pakeman 2001).

It is possible to speculate that these populations are a relic of past grazing patterns. It is known that cattle were widely grazed at altitude during the summer months in the Scottish Highlands in past centuries. Historical records show cattle grazing near the south top of Beinn a' Bhuird (1177 m)

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[1] Interestingly Beinn a' Bhuird has the highest recorded *Calluna* plant in Britain at 1095 m a.s.l. (Pearman & Corner 2003).

as late as ca. 1870s (New Statistical Account). This may have provided a means of dispersal for *Calluna* seeds, as well as for graminoid species (Welch 1985, Welch *et al*. 1990). This combination of potentially greater nutrient availability and graminoid cover may have led to favourable conditions for *Calluna* establishment (Bayfield 1996). Changes in grazing patterns may have resulted in the loss of the short lived graminoid population, leaving relic populations of the longer lived *Calluna* and its seedbank.

Non *Calluna* species

Overall there is very little seed currently arriving from outwith the trapping stations or outwith the sites (transects), showing that most seed is indeed deposited within a few metres of the parent plant. The few seeds which were most likely to have travelled long distances were those which have adaptations for wind dispersal, i.e. *Betula nana* and C*irsium* sp. No vagrant seed was found from outwith the site above 900m, except for thistle down (*Cirsium* sp.).

The numbers of non *Calluna* seedlings recorded emerging from the seedbank were far smaller than *Calluna*. There were a few vagrant species such as *Poa annua*, but this graminoid species was only represented by one seedling and is short lived in the seedbank (Bayfield *et al*. 1984). There were also some seedlings recorded which are rarely found in the seedbank such as *Empetrum nigrum* and *Vaccinium myrtillus*, these are principally dispersed by endozoochory (Welch 1985, Welch *et al*. 2000). None of these seedlings would by themselves represent a potential for a shift in vegetation zone, as most were within their current altitudinal distribution.

There was one *P. sylvestris* sapling recorded in the vegetation survey at 750 m on Derry Cairngorm, this is however not sufficient to suggest a rise in the tree line. While it is referred to here as a seedling, this is not a reflection of its age. Unfortunately it was too small to age by non destructive techniques, but it is possible that this plant had been here for some considerable time. There have been a number of reports of *P. sylvestris* being found at altitudes of up to 850 m in the Cairngorms for the last 40 years (Bayfield *et al*. 1998), so this was not unexpected.

C. bigelowii seedlings were observed emerging from the seedbank at lower altitudinal levels than was recorded in the vegetation survey. However *C. bigelowii* can persist in seedbanks for in excess of 200 years (Brooker *et al*. 2001). Also seed dispersal is wind driven and can take place over long distances when the seeds are blown over snow (Brooker *et al*. 2001). The seedbank densities recorded at the four sites (Table 2.7) are similar to those reported in Alaska and Iceland (Brooker *et al*. 2001).

One species was notable by the low level of its presence as seedlings in the seedbank, *Juncus trifidus*. Seedlings of this species were only recorded at a few trapping stations despite being well represented in the seed rain caught in the seed traps. Little is known of longevity in the seedbank, it is however noted as a sparse coloniser (Bayfield *et al*. 1984, Bayfield 1996).

2.4.2. Factors influencing vegetation under climate change

It has been suggested that global climatic change may increase seed shed and germination (Miller & Cummins 2001). Low temperatures are known to affect germination rate in *Calluna*, as the seeds do not germinate at temperatures below 10˚ C (Cummins & Miller 2002). The optimal constant temperature for germination of seeds of *Calluna* is 20˚ C, and freshly shed seed requires several days of relatively high temperatures in order to geminate (Cummins & Miller 2002). It should be noted that soil temperatures can be 1-2˚ C warmer than air temperature in winter and cooler in summer (Green & Harding 1980). However, *Calluna* seedling survival at higher altitudes is known to be poor (Legg *et al*. 1992, Bayfield *et al*. 1984) due to sporadic snow cover leading to frost heave (Legg *et al*. 1992) and increased wind exposure (Miller & Cummins 1987). Given current predictions of declining snow cover in future years due to climate change (Hulme et al.

2002), this is could lead to a slow decline in seedbank density due to increased germination followed by seedling mortality.

For species other than *Calluna* there is far less published information available. *Erica cinerea* (L.) and *Juncus squarrosus* (L.) both produce less seed with increasing altitude (Miller & Cummins 1976), as does *Nardus stricta* (L.) (Miller & Cummins 1981) particularly in the west of Scotland (Miller & Cummins 1976).

According to Miller and Cummins (2001), annual fluctuations in the seed set of *Calluna* at altitudes below 600 m vary quite widely, and at higher altitudes this inter-annual variation is more pronounced. The main factors found to influence seed set at higher altitudes are temperature and wind speed, with cool windy summers reducing the activity of invertebrate pollinators and also the growth of the pollen tube (Gimingham 1960, Mahy *et al*. 1998, Miller and Cummins 2001). Water shortage can also reduce seed set although this may be less important at higher altitudes in Scotland. It is not just *Calluna* which is affected by cool and wet summer weather. Molau and Larsson (2000) found that in Swedish Lapland the cool wet summer of 1995 substantially reduced seed set in all functional groups, particularly in graminoids and herbs. However in this study there was insufficient data to test this for the non *Calluna* species.

In the current study a large variation was observed in the seed rain between the two years of seed collection. This may be due to the weather during the summers of 2002 and 2003 being very different in nature (Table 2.13). The summer of 2002 was cool and unusually wet, whereas the summer of 2003 was warm and unusually dry[2]. This would explain the lower rates of seeds collected from the seed traps in 2003 compared with 2002 at most trapping stations. Overall the seed rain was higher for all sites in the 2nd year of seed trapping.

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[2] Globally, 2002 and 2003 were respectively the 2nd and 3rd warmest years since records began (Lowe *et al.* 2003, 2004)

Table 2.13. Regional mean maximum and mean minimum temperatures, and mean rain fall for the summers (Jun – Aug) of 2002 and 2003 for the East of Scotland. (Source: Metrological Office web site www.met-office.gov.uk).

Year	Max °C	Min °C	Sun shine hrs	Rain mm
2002	16.8	9.3	373.9	347.6
2003	18.6	9.9	522.9	138.4

2.4.3. Influences other than climate change

While the emphasis of this study is on climate change, it has to be remembered that influences other than climate could be responsible for some of the patterns observed in the data. At the Glas Maol and Glas Tulaichean sites, lower levels of both *Calluna* seed rain and seed bank size were recorded. For instance, a far lower capture of seed rain than at the other sites was observed on Glas Maol (the exception being at 750 m, see below), with mean annual densities of less than 350 seeds m^{-2} at all altitudes. This compares with mean annual seed densities of 3000-4000 m^{-2} at the lower altitudes on Beinn a' Bhuird and Derry Cairngorm. This is probably due to grazing pressures, as the Glas Maol and Glas Tulaichean sites are currently grazed by sheep, whereas the other two sites are not. This grazing by sheep may have reduced the seed input to the seed bank, as well as being responsible for the reduced seed rain.

At 750 m on Glas Maol the largest seedling count of all stations by far was recorded. This is possibly due to soil conditions, as the soil there was deep peat which is known to have an effect on the density and longevity of the *Calluna* seedbank (Legg *et al.* 1992, Cumming & Legg 1995, Miller & Cummins 2003).

2.4.4. Uncertainties

Determining the how far seeds can travel is notoriously difficult (Bullock & Clarke 2000, Greene & Calogeropoulos 2002). Possibly the trapping effort was too small, but then seed was not the seen at stations with plants which would have been expected to produce seed. So there can be reasonable confidence in these results.

There are always problems with the estimate of seedbank density (Miller & Cummins 2003), such as soil collection and processing methods, as well as timing with regard to the seed shed of the investigated species. In this study the collection of soil was much later in the year than Miller and Cummins (1987) and Cummins and Miller (2002). However it was still before most of the current year's seed shed above 700 m a.s.l., which occurs between late December and early June at these altitudes (Cummins and Miller 2002). It should also be noted that the summer before the soil cores were collected (2002) was cold and wet, so the probability of seedling emergence depleting the seedbank was low, as *Calluna* seedlings do not germinate at soil temperatures below 10℃ (Grime *et al*. 1981, Cummins and Miller 2002).

2.5. Conclusions

The results from the seed trapping suggest upward seed movement is limited and so any upward migration of lower vegetation zones, either *Calluna* or other vascular plants will be very slow. However, the study also showed that there is a small *Calluna* seedbank above the vegetation zone where *Calluna* is currently the dominant plant. However it is questionable whether the seedbank would enable *Calluna* to colonise higher altitudes, because of high seedling mortality. While it has not been possible to determine during this study if there have been any changes in the nature of the seedbank over recent decades, the size of the *Calluna* seedbanks reported from the 1970's and 1980's (Miller & Cummins 1987, Cummins & Miller 2002) is similar to that found by this study.

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