# Long-term changes in the size of an Alpine Gentian, *Gentiana nivalis* L., population in Scotland

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ABSTRACT

The density of *Gentiana nivalis* (Alpine Gentian) plants in herb-rich grassland at Ben Lawers, Perthshire had been much reduced after ten years of artificial protection from summer grazing by large herbivores. The restoration of summer grazing from 1997 resulted in a partial recovery by 2006. The recovery of this annual species was associated with an increase in the amount of bare soil, so providing seed beds essential to the establishment of new plants. Thus grazing and trampling are clearly important elements in the conservation of *G. nivalis* populations in herb-rich grassland.

Where sheep had been allowed to graze each summer from 1987 to 2006, an overall decline in the *G. nivalis* population size was coincident with a progressive increase in the height of perennial plants. Over the same period, the climate became warmer, wetter and there was less snow. There is no convincing evidence of a direct effect of this climate change on the *G. nivalis* population. However, warm, wet springs have apparently encouraged the growth and spread of perennial vegetation to the detriment of *G. nivalis* establishment. Plants on incompletely vegetated cliff ledges have not been so affected, presumably because they are less exposed to competition from perennials.

KEYWORDS: climate change, grazing, herb-rich grassland, montane annual, competition.

## INTRODUCTION

This paper documents changes observed in the size of a *Gentiana nivalis* L. (Alpine Gentian) population in grazed herb-rich grassland and considers possible causes. *G. nivalis* is a rare montane annual, regarded as 'vulnerable' (Wigginton 1999). The main British population is located near to the summit of Ben Lawers, Perthshire, Scotland (56º33'N, 4º14'W). Here it grows on partially vegetated cliff ledges as well as on grazed, herb-rich grassland below. Geddes (1996) identified the cliff vegetation as the *Dryas octopetala-Silene acaulis* ledge community, CG14 in the National Vegetation Classification (Rodwell 1992), whilst the grassland is the *Festuca ovina-Alchemilla alpina-Silene acaulis* dwarf herb community, CG12. Other small *G. nivalis* colonies occur on nearby hills as well as at a more distant site, Caenlochan Glen, Angus.

Grazing by sheep is a major cause of mortality amongst *G. nivalis* plants in the grassland at Ben Lawers (Batty *et al.* 1984). Despite this, it appeared that sheep might actually help to sustain the population by repeatedly cropping perennials and by creating seed beds through their trampling. Confirmation came from an experimental study in 1987–1996 (Miller *et al.* 1999) which showed that protection from summer sheep-grazing resulted in an appreciable reduction in *G. nivalis* numbers. Plant numbers on the 'control' plots grazed by sheep each summer also declined over the ten years of the experiment, though the trend was less conspicuous and not statistically significant.

Sheep-grazing was restored from 1997 onwards and changes in *G. nivalis* population size were recorded for a further ten years. The aims here were (a) to establish the extent of any recovery on the previously ungrazed 'test' plots, and (b) to investigate further the apparent decline on the 'control' plots which were always grazed.

At Caenlochan Glen, many years of heavy grazing by red deer (*Cervus elaphus* L.) are thought to have caused the decline and recent disappearance of *Gnaphalium norvegicum* Gunnerus (Highland Cudweed) and *Cicerbita alpina* (L.) Wallr. (Alpine Blue-sow-thistle) in an adjacent glen (Geddes & Payne 2006).

In view of the vulnerability of *G. nivalis* at this location, a small population has been counted annually from 1982 to 2006. These observations are also recorded here and compared with those from Ben Lawers.

## METHODS

### BEN LAWERS

The study area has been described by Miller *et al.* (1999) in terms of its location, vegetation, soils and vertebrate herbivores.

Data recording in 1997–2006 was similar to that already described (Miller *et al.* 1999) for the preceding ten years. In summary, eight pairs of permanently-marked plots, established in July 1987, were examined every summer over a period of 3–5 days in late-July or early-August. Each plot was 70 cm × 50 cm. One plot of each pair remained as the 'control', i.e. open to sheep-grazing each summer since 1987. The nearby 'test' plot was no longer protected from grazing by sheep, i.e. previously-ungrazed plots were now exposed to the same treatment as the control plots. In each plot, *G. nivalis* plants were recorded and their flowers counted. In addition, the mean height of the perennial vegetation was obtained from 20 measurements per plot and the percentage cover of bare soil, as defined by Miller *et al.* (1999), recorded.

### CAENLOCHAN GLEN

At Caenlochan Glen the location of the small *G. nivalis* population under study is on a steeply sloping west-facing outcrop that is not readily accessible to sheep or red deer. Perennial vegetation occupies about 60% of the site whilst bare soil, gravel and rock accounts for the remaining 40%.

A 1 m × 1 m permanent plot was established here in August 1982. The number of *G. nivalis* plants was counted in late-July or early-August every year from then until 2003. In 2004–2006, counting was in late-August or early-September.

### ANALYSIS AND PRESENTATION OF DATA

Trends in the population size of *G. nivalis* with the passage of time were examined by linear regression analysis. On the Ben Lawers test plots, the ungrazed period, 1987–1996, and the subsequent grazed period, 1997–2006, were analysed separately. On the control plots, the entire data set for 1987–2006 was used in a single calculation. In these analyses, the number of years that had elapsed since 1987 was taken as the independent variable, with *G. nivalis* density (transformed to $\log_e$) as the dependent variable. The data for the single plot at Caenlochan Glen were analysed in the same way.

The significance of the regression coefficients was assessed by t-test. Similar analyses were undertaken for vegetation height and for the amount of bare soil at Ben Lawers.

## RESULTS

### DENSITY OF *GENTIANA NIVALIS* PLANTS

In 1987–1996, when protected from sheep-grazing, the mean density of *G. nivalis* plants on the test plots at Ben Lawers decreased steeply, at a rate of 0·24 plants per plot per year (Fig. 1a). After restoration of grazing in 1997, plant density increased over the following nine years at a rate of 0·08 plants per plot per year (Fig. 1a). Thus recovery was much slower than the decline.

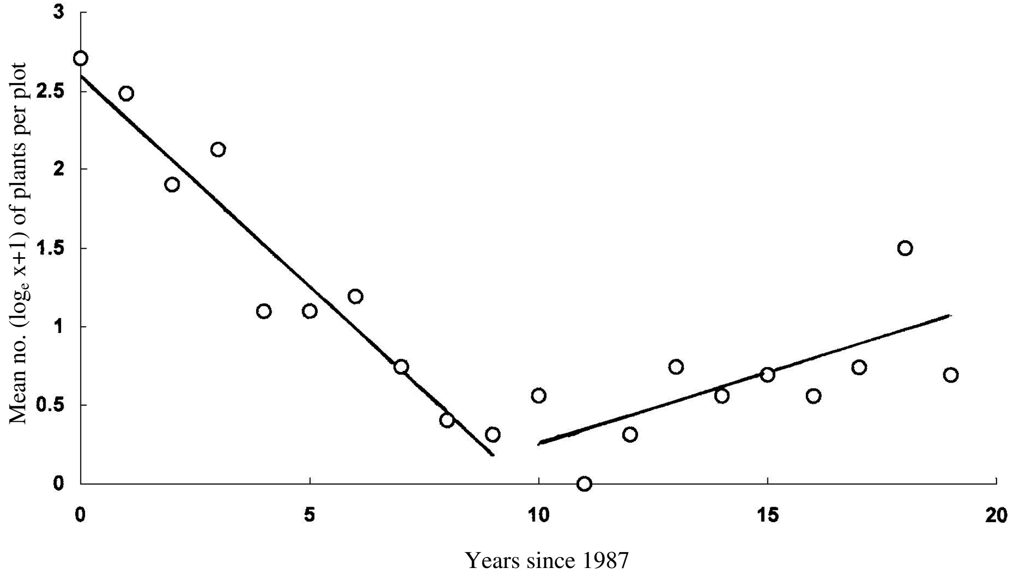
Figure 1b shows that fluctuations in mean *G. nivalis* density at Ben Lawers had greater amplitude on the control plots than was the case on the test plots. Nevertheless the steady decline previously observed in 1987–1996 continued through 1997–2006. There is no significant difference in the slopes of the regressions for these two periods and the overall rate of decline over 20 years is 0·6 plants per plot per year.

As on the control plots at Ben Lawers, the number of *G. nivalis* plants on the single plot at Caenlochan Glen fluctuated widely, from none in 1995–1996 to 73 plants in 1982 (Fig. 2). In fact the population fluctuations at these two sites are broadly synchronous as they are positively correlated ($r = +0{\cdot}46$, $p = 0{\cdot}040$). However, at Caenlochan Glen there is no evidence of any consistent reduction in population size over the 25-year period.

### AMOUNT OF BARE SOIL AT BEN LAWERS

When protected from sheep-grazing, the mean cover of bare soil in the test plots decreased sharply, from 4·3% in 1987 to 0·25% in 1996 (Fig. 3a). Restoration of grazing resulted in an equally rapid increase to 7·7% in 2006, although the extent of this recovery was exaggerated due to a massive rock fall at one of the plots early in 2006. By contrast there was no consistent trend in the amount of bare soil in the control plots where it varied between 5·3% and 11% (Fig. 3b).

(a) Ungrazed 1987–1996, grazed 1997–2006




(b) Grazed 1987–2006

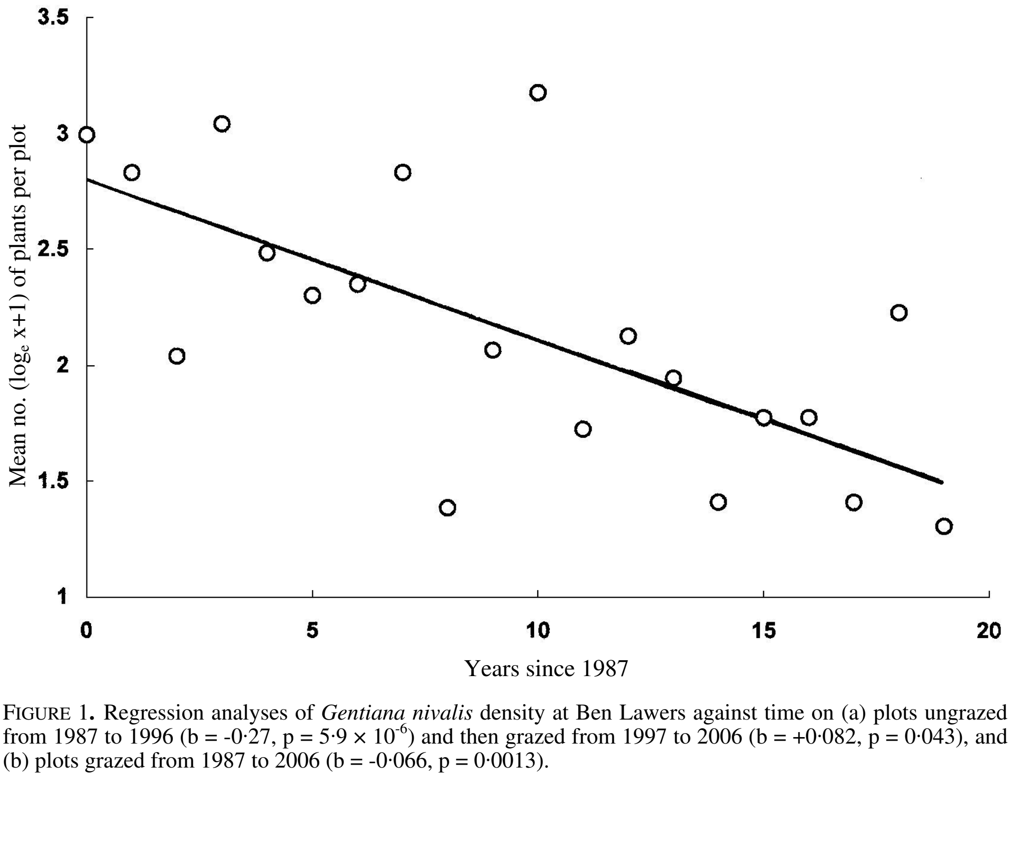



FIGURE 1. Regression analyses of *Gentiana nivalis* density at Ben Lawers against time on (a) plots ungrazed from 1987 to 1996 ($b = -0{\cdot}27$, $p = 5{\cdot}9 \times 10^{-6}$) and then grazed from 1997 to 2006 ($b = +0{\cdot}082$, $p = 0{\cdot}043$), and (b) plots grazed from 1987 to 2006 ($b = -0{\cdot}066$, $p = 0{\cdot}0013$).

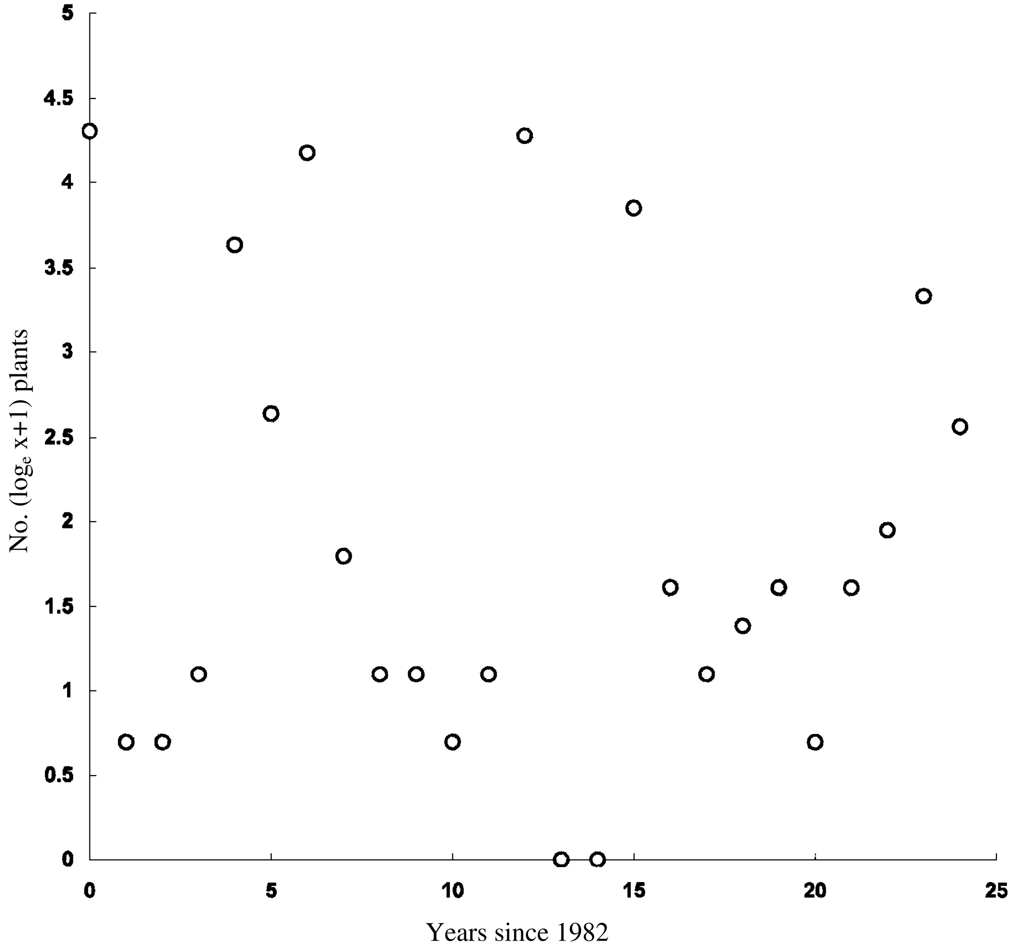



FIGURE 2. Regression analysis of *Gentiana nivalis* density at Caenlochan Glen against time on a single plot open to grazing from 1982 to 2006 (b = -0·075, p = 0·72).

HEIGHT OF PERENNIAL VEGETATION AT BEN LAWERS

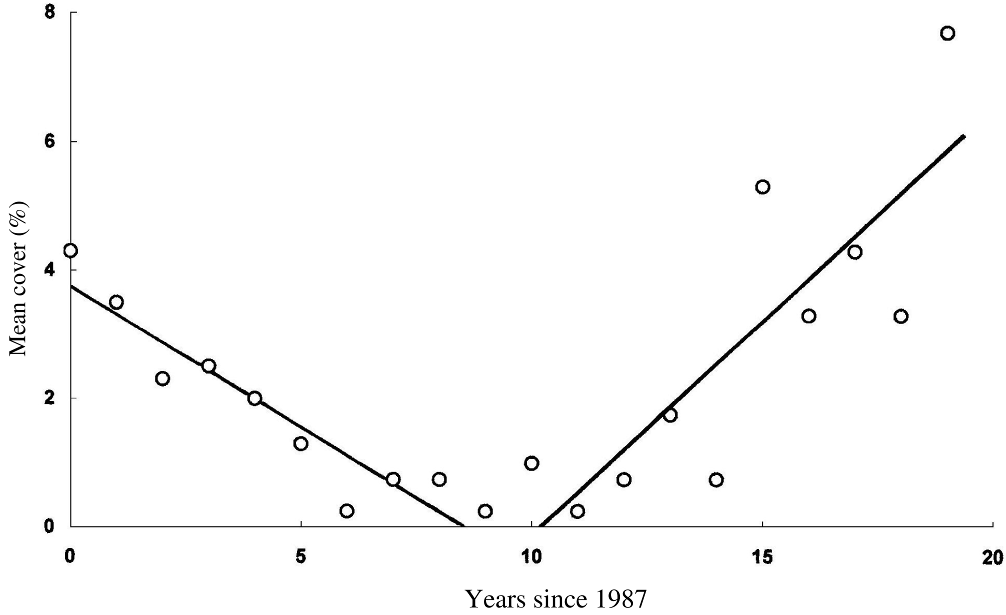
Protection from sheep-grazing resulted in an almost doubling of the mean height of perennial vegetation between 1987 and 1996 (Fig. 4a). Restoration of grazing reversed this trend. On the control plots, a sustained increase in height of approximately 1 mm per year occurred so that by 2006 the perennial vegetation stood approximately 20 mm taller than it did in 1987 (Fig. 4b).

## DISCUSSION

BEN LAWERS TEST PLOTS

Miller *et al.* (1999) concluded that losses from the *G. nivalis* population on plots protected from sheep-grazing might have been caused primarily by a decline in the amount of bare soil, thus resulting in the decreased availability of suitable seed beds. The number of seed capsules formed in the previous year was another possible factor. Although seed availability is clearly important, large numbers are produced annually (Miller *et al.* 1999; Miller & Geddes 2004) and there is a large long-lived seed bank (Miller 2004). Thus it seems likely that it was the rapid increase in the amount of bare soil following the restoration of grazing on the test plots (Fig. 3a) that accounted for the partial recovery of the *G. nivalis* population. This confirms a previous conclusion (Miller *et al.* 1999) that grazing and trampling by sheep, and possibly also by red deer, are crucial in sustaining this species in herb-rich grassland.

(a) Ungrazed 1987–1996, grazed 1997–2006




(b) Grazed 1997–2006

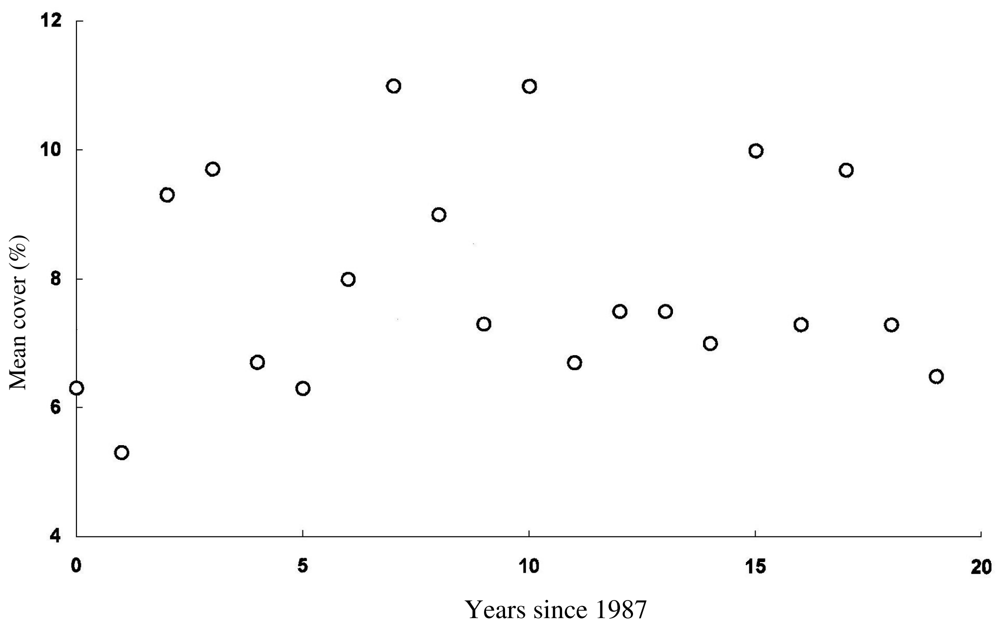
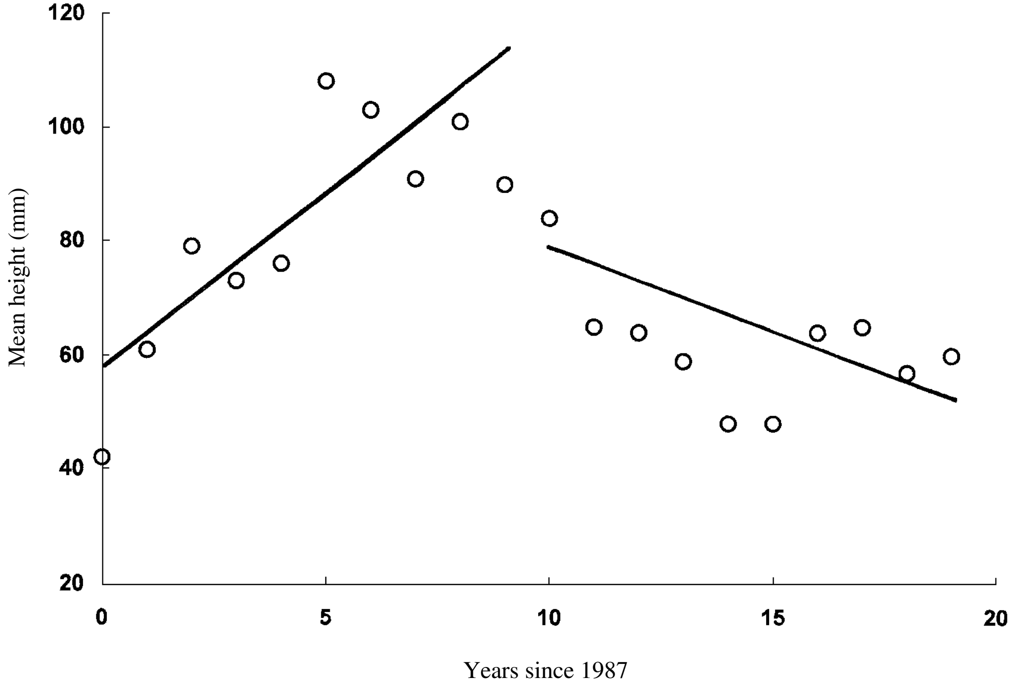



FIGURE 3. Regression analyses of amount of bare soil in July at Ben Lawers against time on (a) plots ungrazed from 1987 to 1996 (b = -0·43, p = 0·00047) and then grazed from 1997 to 2006 (b = +6·6, p = 0·0032), and (b) plots grazed from 1987 to 2006 (b = +0·023, p = 0·73).

(a) Ungrazed 1987–1996, grazed 1997–2006




(b) Grazed 1997–2006

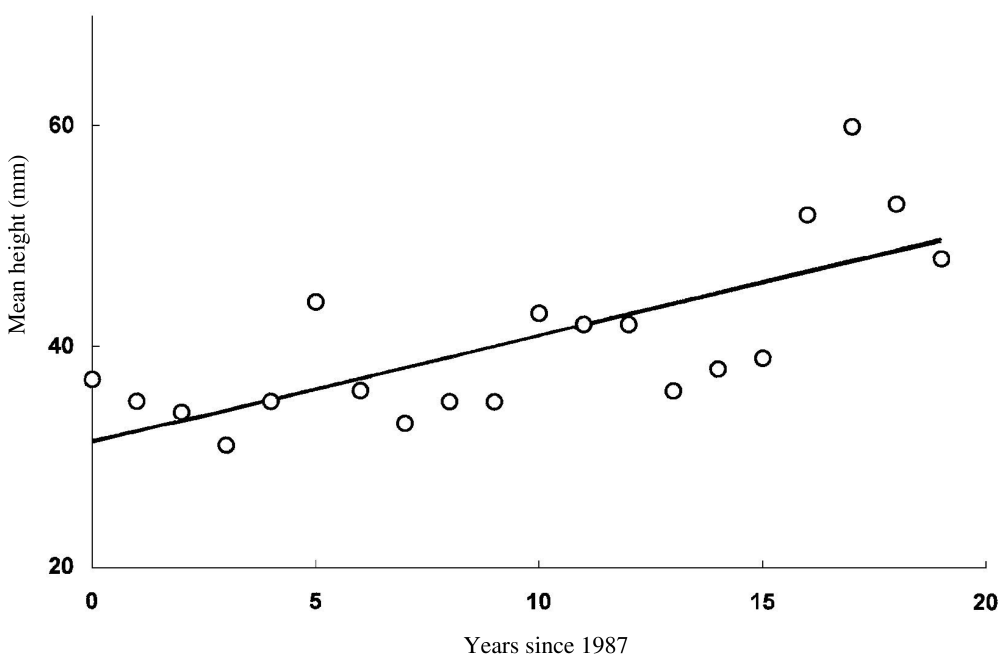



FIGURE 4. Regression analyses of height of perennial vegetation in July at Ben Lawers against time on plots ungrazed from 1987 to 1996 (b = +5·4, p = 0·0055 and then grazed from 1997 to 2006 (b = -2·4, p = 0·039), and (b) plots grazed from 1987 to 2006 (b = +0·93, p = 0·00034)

The incomplete recovery of *G. nivalis* numbers on the test plots is perhaps unsurprising given that numbers were simultaneously decreasing on the control plots. Presumably factors causing these losses must have been operating on both sets of plots.

BEN LAWERS CONTROL PLOTS

Big fluctuations in *G. nivalis* numbers have long been recorded from Ben Lawers and from the adjacent hills (Batty *et al.* 1984; Geddes 1992; Miller *et al.* 1999). However, the variability at Caenlochan Glen in 1982–2006 seems to be around a long-term mean level which neither increased nor decreased (Fig. 2). In contrast, the 20-year decline in the population size of *G. nivalis* at Ben Lawers (Fig 1b) is indisputable and may threaten the long-term survival of the species in the herb-rich grassland.

Where grazing had continued normally in 1987–1996, Miller *et al.* (1999) concluded that variations in seed production in the preceding autumn and the height of the perennial vegetation in the current year may have controlled *G. nivalis* establishment. The possible role of seed availability has been discussed and discounted above. On the other hand, competition from tall vegetation for space, light, water and nutrients is likely to reduce germination and seedling establishment. On the control plots, perennial vegetation became steadily taller from 1987 to 2006 (Fig. 4b) as the density of *G. nivalis* declined. Indeed, there is a broad inverse correlation between these two parameters ($r = -0{\cdot}42$) but it is barely significant ($p = 0{\cdot}064$).

INFLUENCE OF GRAZING

Signs or sightings of red deer were never noted at the Ben Lawers study area and those of mountain hares (*Lepus timidus* L.) rarely so. Grazing impacts were largely due to sheep. Records of sheep density on Ben Lawers during the last few decades have always remained as ‘estimates’, ranging from 1·0 to 2·5 animals $ha^{-1}$ throughout July–August (Batty *et al.* 1984; Miller *at al.* 1999; Dayton 2007). At the study area 2–4 ewes, each with a single lamb, were usually seen from 1987–2006 during each summer visit of 3–5 days. But single period visits do not provide reliable counts of animals present throughout the summer. On the grazed plots, additional observations of sheep activity (trampling, dunging and the presence of uprooted *G. nivalis* plants) varied little over the 20-year period of summer visits. Furthermore, Dayton (2007) reported a high long-term herbivore impact on those samples of vegetation located nearest the study area and this was attributed mainly to sheep. It has been concluded, therefore, that grazing pressure did not change significantly at the study area during 1987–2006.

INFLUENCE OF PERENNIAL VEGETATION

Small annual species such as *G. nivalis* are likely to be vulnerable to competition from taller perennial species. Thus Kelly (1989) found that short-lived species germinated poorly where the height of surrounding grassland vegetation exceeded 30 mm and that subsequent plant survival was also inversely related to vegetation height. At Ben Lawers, the height of perennial vegetation on the control plots increased steadily from about 30 mm in 1987 to about 50 mm by 2006 (Fig 4b).

*G. nivalis* germinates and establishes itself at two separate seasons (Batty *et al.* 1984). Plants that establish in autumn, when perennial vegetation is fully grown and competition is maximal, survive over winter and mostly develop into tall, multi-flowered individuals in the following year. Spring establishment, on the other hand, usually yields small, single-flowered plants which will be less subject to competition from perennial vegetation that is yet to begin to grow.

Correlations between the numbers of single- and multi-flowered *G. nivalis* plants and the height of perennial vegetation in the same and in the previous July are all negative (Table 1). The association between multi-flowered plants and the previous summer’s vegetation is significant, implying that competition from tall perennial vegetation might limit autumn establishment. All other correlations are insignificant although that between single-flowered plants and the current summer’s vegetation is suggestive. However a strong correlation here would be unexpected as the height of perennial vegetation in July would not closely reflect its height in the spring of the same year when growth is just beginning.

Therefore increasing competition from perennial vegetation seems the most likely explanation for the gradual loss of *G. nivalis* plants. Indeed, no overall decrease in *G. nivalis* density was recorded at two other sites with much bare ground and only scattered perennial vegetation – Caenlochan Glen (Fig. 2) and an ungrazed rock outcrop at Ben Lawers (Geddes 2008).

TABLE 1. CORRELATIONS BETWEEN HEIGHT OF PERENNIAL VEGETATION IN JULY AND DENSITY OF SINGLE-FLOWERED AND OF MULTI-FLOWERED *GENTIANA NIVALIS* PLANTS

| No. of flowers per plant | Height of perennial vegetation in current July | | previous July | |
|---|---|---|---|---|
| | r | p | r | p |
| 1 | -0·38 | 0·097 | -0·25 | 0·29 |
| 2+ | -0·34 | 0·14 | -0·56 | 0·013 |

INFLUENCE OF CLIMATE

Associations between the fluctuations in *G. nivalis* density in 1987–2006 and climatic variation at Ben Lawers were explored using data from Ardtalnaig Meteorological Station ($56^0$32’N, $4^0$07’W). Although located some 7 km from the study area and 900 m lower in altitude, it has been assumed that the meteorological data would reflect differences amongst years near the summit of Ben Lawers. Three climatic variables were examined – air temperature, precipitation and number of snow/sleet days (Meteorological Office, pers. comm., 2008). These parameters showed clear trends during 1987–2006 of warming temperature, increasing precipitation and fewer days with snow, which accords with climate scenarios predicted for the UK (Hulme & Jenkins 1998).

Climatic variation could influence the population size of an annual species in three ways (Levine *et al.* 2008): (i) direct effects on germination and establishment, (ii) direct effects on established plants, and (iii) indirect effects mediated by the surrounding vegetation. Hence correlations were sought between the mean number of single-flowered and of multi-flowered *G. nivalis* plants on the Ben Lawers control plots and (a) temperature and rainfall during the two main germination periods, August–September and May–June (Batty *et al.* 1984), (b) temperature and rainfall during the main growing period, May–August, and (c) the number of snow/sleet days in October–May, which might influence the survival of plants established in autumn (Miller & Geddes 2004). Despite the general warming trend concurrent with the decline in *G. nivalis* numbers, none of these climatic variables, either singly or in combination, provide a statistical explanation.

No specific information on the amount and duration of snow cover is available for either the Ben Lawers or the Caenlochan Glen study areas. However, a survey of the number and size of summer snow patches in north-east Scotland (Watson *et al.* 1994) includes data for 1982–1989 when *G. nivalis* plants were counted at Caenlochan Glen. There is no evidence of any relation between snow cover and *G. nivalis* density during that period. Yet the synchrony between the fluctuations at Ben Lawers and those at Caenlochan Glen, about 65 km away, suggests that some aspect of year-to-year climatic variation is a contributory factor. Unmeasured variables such as soil temperature or the depth of winter snow-lie might be important here.

There is, however, a clear association between annual variations in the height of perennial vegetation in the grazed plots at Ben Lawers in 1987–2006 and the mean minimum temperature ($r = +0{\cdot}62$, $p = 0{\cdot}0035$) and total precipitation ($r = +0{\cdot}50$, $p = 0{\cdot}026$) in April–June, the beginning of the growing season at 1000 m altitude. Increasing heat and moisture in spring seems a plausible explanation for the long-term increase in vegetation height on the study area.

It therefore seems reasonable to conclude that some unknown climatic factor might account for the year-to-year fluctuations in the population size of *G. nivalis* plants. However the overall decline in population size in the Ben Lawers control plots can be explained as an indirect effect of climate change mediated by the enhanced growth of perennial vegetation. Climate change during the 20-year monitoring period seems to have had an impact similar to that produced by protection from grazing in 1987–1996, namely an increase in the height of perennial vegetation with a consequent loss of *G. nivalis* habitat. If the present climatic trends continue, the survival of the *G. nivalis* population in herb-rich grassland at Ben Lawers must be in doubt. By contrast, plants on partially vegetated cliff sites appear to have been unaffected so far.

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