Population age structure and recent *Dracophyllum* spread on subantarctic Campbell Island

Kim L. Bestic[1,2], Richard P. Duncan[1,3,*], Matt S. McGlone[3], Janet M. Wilmshurst[3] and Colin D. Meurk[3]

[1] Bio-Protection and Ecology Division, P.O. Box 84, Lincoln University, Canterbury, New Zealand
[2] Present address: Jed Vale, Gore Bay, R.D. 3 Cheviot, North Canterbury, New Zealand
[3] Landcare Research, P.O. Box 69, Lincoln, New Zealand
* Author for correspondence (E-mail: duncanr@lincoln.ac.nz)

Abstract: Mid to late 20th century expansion of *Dracophyllum* scrub into tussock grassland on subantarctic Campbell Island has been attributed to the collective effects of global warming, cessation of farming in 1931, and continued grazing by feral sheep. To determine the importance of these, we dated the timing of scrub expansion by aging 241 *Dracophyllum* plants in 17 plots chosen to sample the range of environments this shrub/ small tree occupies on Campbell Island. Three plots, in lowland, well-drained, locations were dominated by large, old *Dracophyllum* that had established between 1846 and 1940. Virtually all shrubs in the remaining plots had established after 1940, with peaks in 1970 and 1985. The pattern of establishment does not coincide with any marked change in the temperature regime, although a prolonged period of relatively dry winters (*c.* 1970–1990) coincides with a late surge of regeneration on very wet sites. The removal of feral sheep from different parts of the island at different times is also unrelated to the pattern of establishment. In contrast, *Dracophyllum* spread follows farm abandonment in 1931 when regular burning ceased, suggesting that *Dracophyllum* is invading sites from which it was excluded by fire. However, the earliest reports from the mid 19th century indicate that tussock grassland was previously the dominant vegetation cover on the island, with limited *Dracophyllum* scrub. It is possible that the reduction of the dense tussock grasslands by fire and grazing in late 19th–early 20th century opened a regeneration window for *Dracophyllum* scrub to spread once burning ceased.

Keywords: climate warming; land-use change; treeline; tree spread; invasion; fire; grazing; subantarctic islands

Introduction

Woody vegetation is expanding in many areas, in particular at high latitudes and at alpine treeline in the northern hemisphere, a phenomenon often attributed to global warming (Lescop-Sinclair and Payette, 1995; Dullinger *et al.*, 2004). However, evidence for such change is equivocal on the New Zealand mainland (Wardle and Coleman, 1992; Cullen *et al.*, 2001). Subantarctic Campbell Island (Fig. 1), 600 km south of the New Zealand mainland, provides an ideal opportunity to investigate the reaction of woody vegetation to global warming. Woody vegetation is at its southern latitudinal limit in the western South Pacific on Campbell Island and its alpine treeline is the lowest in the region. The climate is highly oceanic, cool (mean annual temperature at sea level 6.8°C), wet (1400 mm over 250 rain days) and very windy (de Lisle, 1965; NZMS, 1973; Meurk and Blaschke, 1990). All but a small proportion of the soils are deep, highly organic peats. Tussock grassland, tundra or macrophyllous forbs dominate above 200 m a.s.l and on the exposed western side of the island (Meurk *et al.*, 1994). Below 200 m and in sheltered leeward valleys, the vegetation is dominated by taller *Dracophyllum longifolium* and *D. scoparium*, and scrub of *Dracophyllum*, *Coprosma* spp. and *Myrsine divaricata*, aside from extensive tracts of oligotrophic cushion bog on broad interfluves. *Dracophyllum longifolium* and *D. scoparium* are the two primary small tree-tall shrub species on the island. *D. longifolium* favours warmer, more sheltered, better drained sites where it can grow to a height of 5 m; *D. scoparium* is generally of lower stature and can extend its range onto poorly drained oligotrophic bogs, but as a stunted shrub (Meurk *et al.*, 1994). The two species form a hybrid swarm. Both are vulnerable to fire but unpalatable to sheep.

Campbell Island vegetation should thus be a highly sensitive indicator of warming in the New Zealand region. In fact, scrub cover has increased since the middle of last century, and it has been suggested that

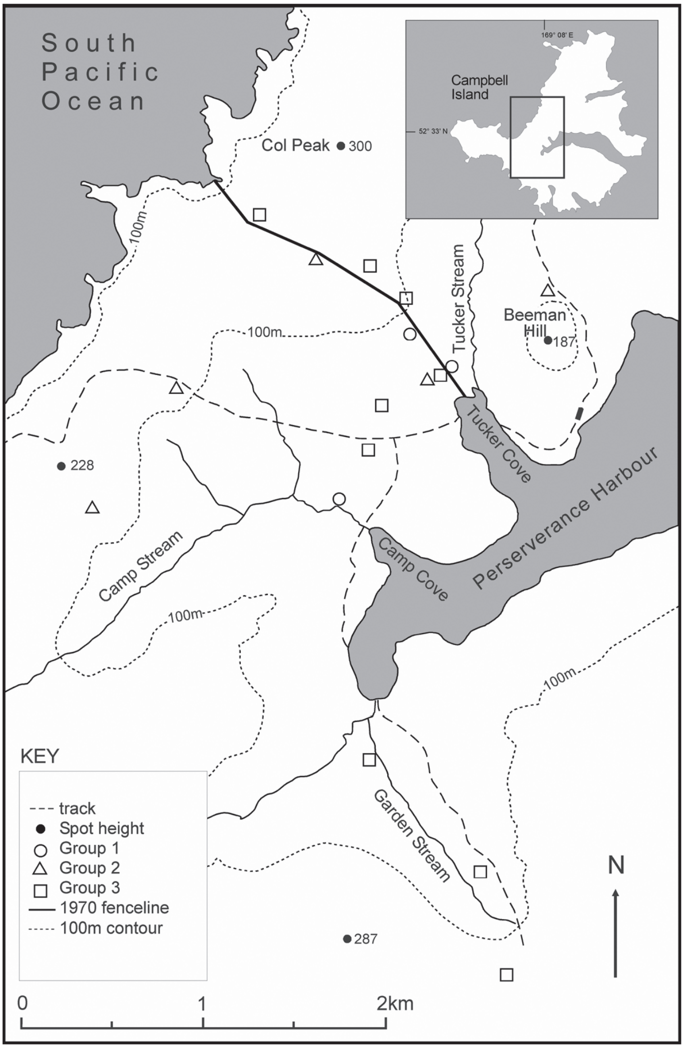

Figure 1. Map of the study area on Campbell Island showing major features and the plot locations, with different symbols indicating the groups that plots were assigned to by cluster analysis on the basis of similarities in age structure (see text and Fig. 3).

global warming in this region has assisted its spread (Meurk, 1982; Rudge, 1986; McGlone *et al.*, 1997; Wilmshurst *et al.*, 2004). The first vegetation descriptions of the island (Hooker, 1844; Buchanan, 1883) recorded scrub being largely confined to sheltered gullies and the shoreline. Elsewhere there were tussock grasslands and herbfields dominated by *Chionochloa antarctica* and *Bulbinella hookeri*. However, scattered trees and shrubs occurred within these grasslands at least up to the current altitudinal limit for coextensive *Dracophyllum* scrub (200–250m: Meurk and Given, 1990; McGlone *et al.*, 1997). Absolute limits for *Dracophyllum* shrubs are 300–400 m (C. Meurk, pers. obs). Later reports (Cockayne, 1903; Zotov, 1965) confirm that scrub remained restricted until the 1950s. An analysis of photographic sequences spanning the period 1888–1998 (Wilmshurst *et al.*, 2004) shows that the cover of lowland *Dracophyllum* scrub has expanded dramatically over the last century, with the rate of increase highest in the second half of the century. This increase in woody vegetation on the island coincides with a shift to warmer, drier climates in the second half of the twentieth century.

Despite this apparent correlation with warming, expansion of woody vegetation on Campbell Island (and in other parts of the world) could be a consequence of changes in other factors. Since European discovery in 1810, Campbell Island has undergone major changes

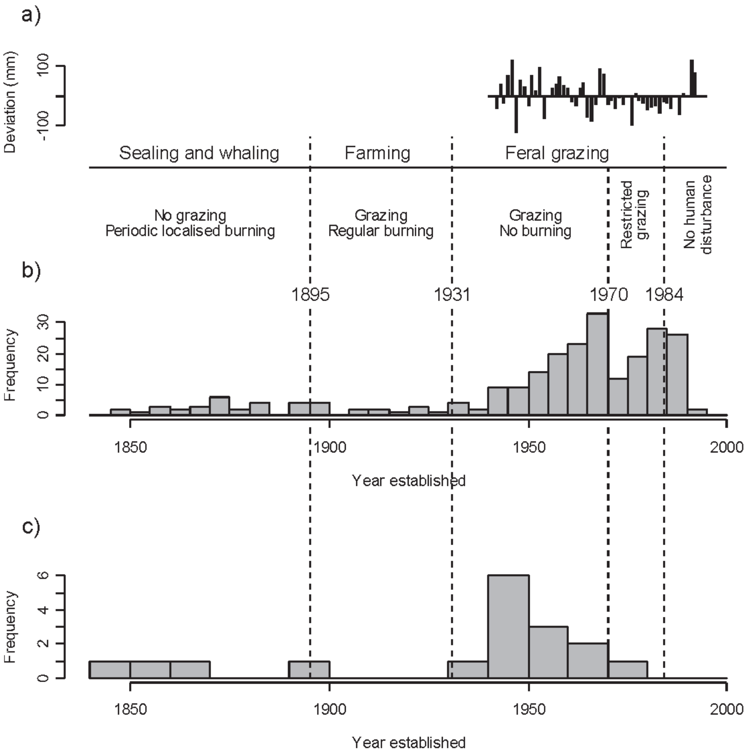

Figure 2. *Dracophyllum* age structures, anthropogenic events, and rainfall trends. a) Deviation from winter mean rainfall (mm) on Campbell Island for the years 1941–95. (from data in Fig. 2 of Wilmshurst *et al.*, 2004); b) frequency distribution of year of establishment (in five-year bins) for 241 *Dracophyllum* plants in 17 plots that we aged on Campbell Island, along with dates in Campbell Island history where there were significant changes in the fire or grazing regimes; c) frequency distribution of the year of establishment (in ten-year bins) of the oldest plant in each plot.

in land-use with associated changes in fire and grazing regimes (Wilmshurst *et al.*, 2004; Fig. 2). Consequently, there are at least three non-mutually exclusive hypotheses that could account for the expansion of scrub on the island over the last century.

First, fire was used episodically by sealers and whalers to clear vegetation beginning at least as early as 1840. Shepherds regularly fired both tussock and scrub for access and to improve grazing when sheep and cattle were introduced to the island in 1895. Burning was part of a regular farming pattern, as is clear from accounts of the years 1919–1921 (Dingwall and Gregory, 2004) and 1929–1931 (Spence, 1968), but ceased in 1931 when farming was abandoned. Repeated fire will exclude many woody plants and recent scrub expansion may reflect an expansion of woody vegetation into areas from which it was excluded by human-caused fires. If this is the case then we should expect major scrub expansion to have commenced after 1931.

Second, farming began in 1895 and sheep numbers peaked in the early 1900s before declining to around 4000 in 1931, when farming ceased and the sheep were left to run feral on the island. Sheep numbers continued to decline until the 1960s and then increased unexpectedly (Rudge, 1986). In 1970 a fence was erected across the waist of the island (Fig. 1) and sheep were eradicated north of the fence. The sheep population south of the fence increased from 2500 in 1970 to 3500 in 1983. A second fence was erected in 1984 restricting sheep to the southwestern-most part of the island, and these remaining sheep were eradicated in 1991. Sheep were known to selectively graze several dominant grass and herb species on the island. By reducing competition and creating openings in herbaceous vegetation, sheep grazing could have created opportunities for regeneration of the unpalatable *Dracophyllum*. If grazing plays the dominant role then we would expect major scrub expansion to coincide with the introduction of sheep around the turn of the century. Furthermore, we would expect *Dracophyllum* regeneration to have slowed following the removal of sheep grazing from different parts of the island at different times (post-1970 north of the first fenceline, and post-1984 south of the first and north-east of the second fenceline).

Third, the climate on Campbell Island has become drier and warmer in the period 1941–1995 (the period for which records are available) and, in particular, there has been a sustained period of low winter rainfall in the two decades from 1970–1990 (Fig. 2a; see also Wilmshurst *et al.*, 2004). *Dracophyllum* tends to favour relatively drier sites for regeneration (Meurk *et al.*, 1994) and the shift to a drier, warmer climate may have triggered scrub expansion. If this is the case, we expect phases of scrub expansion to coincide with periods of drier, warmer climate.

The three hypotheses make contrasting predictions regarding the timing of scrub expansion on Campbell Island. In this paper we use the dates of establishment of 241 *Dracophyllum* plants in 17 plots located around the head of Perseverance Harbour to establish the timing of scrub expansion on the island to test the above hypotheses.

Methods

In December 1998–January 1999, we located 17 plots around the head of Perseverance Harbour to sample *Dracophyllym* scrub (Fig. 1). Two environmental factors exert a major control on Campbell Island vegetation: soil fertility and elevation (Meurk et al. 1994). We located plots in areas that spanned the range of soil fertility conditions from oligotrophic (low fertility and poor drainage; four plots) to mesotrophic (medium fertility and well drained; nine plots) to eutrophic (high fertility and very wet, but without moving water; four plots), and plots spanning the elevation range from near sea level to the limit of coextensive *Dracophyllum* scrub (*c.* 250 m). In addition, five plots were located north of the fence constructed in 1970, from which sheep were eradicated in that year. The remaining plots were located south of the fence and were grazed up to 1984, when sheep were removed from that part of the island.

Large areas of relatively homogeneous vegetation with uniform site conditions were selected for sampling and identified as oligotrophic, mesotrophic or eutrophic based on the associated plant species (see Meurk *et al.*, 1994). Plot centres were then located at random within these homogeneous areas of vegetation and the elevation, slope angle and aspect of each plot recorded.

We aimed to select the 15 closest *Dracophyllum* plants to each plot centre for sampling, although the actual number ranged from 11–17. For each plant we identified the species (*D. scoparium*, *D. longifolium* or a hybrid between the two), measured its height, counted the number of stems and measured the diameter of each stem at ground level using callipers. Discs were taken from all *Dracophyllum* plants with a stem ≥10 mm diameter to estimate age by ring counting (stems were mostly too small to core). For multi-stemmed plants, the largest diameter stem was sampled on the assumption that this was the oldest. Discs were taken by cutting stems off just above the root collar to estimate establishment date.

Dracophyllum discs were glued to boards in the laboratory, then sanded using successively finer grades of sandpaper until the surface was polished and growth rings were clearly visible. Growth rings were counted under a binocular microscope along three equally spaced radii, with the highest count taken to be an individual *Dracophyllum* plant's age. Growth rings were assumed to be annual.

We used cluster analysis to identify groups of plots with a similar age structure to determine if there are consistent differences in the timing or pattern of *Dracophyllum* establishment with respect to differences among plots in characteristics such as soil type, grazing history and elevation. We combined age data from the two *Dracophyllum* species and their hybrids for this purpose because the two species hybridise freely and all but five plants were identified as either *D. scoparium* or a hybrid. For each plot, we counted the number of plants that had established in each decade between 1840 and 2000. We then constructed a similarity matrix (using Euclidian distance as the measure of similarity), expressing how similar each plot is to every other plot in terms of the number of plants that had established in each decade. Plots were then clustered on the basis of this similarity matrix using average linkage clustering, and the resulting dendrogram was used to identify groups of plots with similar age structures. The pattern and timing of *Dracophyllum* establishment was then examined with respect to key dates in Campbell Island history that marked significant changes in the fire or grazing regimes, and to deviations from winter mean rainfall as an index of relative dryness.

Results

The oldest sampled *Dracophyllum* established in 1846 and was 152 years old. The oldest known *Dracophyllum* from the island is ca. 240 years (C. Meurk, pers. obs.). Across all plots, at least one *Dracophyllum* plant had established in each decade between 1840 and 1940 (Fig. 2b). However, the large majority of the 241 plants we aged (195, or 81%) established after 1940, with apparent peaks in establishment around 1970 and 1985.

Clustering plots on the basis of their age structure identified three clear groupings (Fig. 3). The first group comprised three plots on mesotrophic soils with large, old *Dracophyllum* that contained almost all of the plants aged that had established prior to 1940, with no new establishment in these plots since then. The second group comprised five plots (four eutrophic and

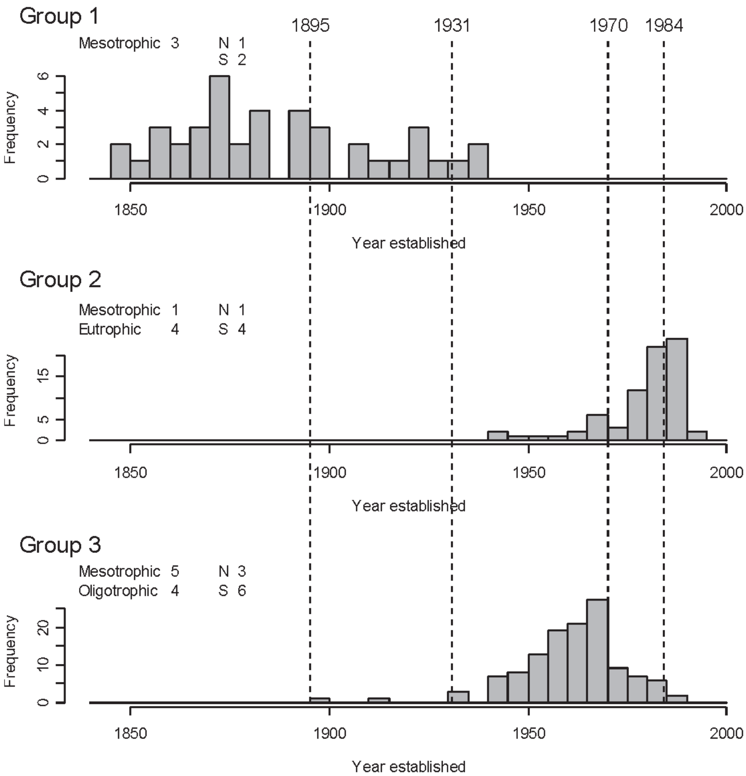

Figure 3. Frequency distributions of the year of establishment (in five-year bins) for *Dracophyllum* plants in each of three groups (1, 2 and 3) obtained by clustering plots on the basis of similarities in their age structure. For each group, the number of plots that were located on the three soil types (mesotrophic, oligotrophic and eutrophic), and the number of plots located north (N) or south (S) of the fence constructed in 1970 are shown, along with key dates in Campbell Island history (see Fig. 2).

one mesotrophic) of predominantly younger plants, most of which had established between 1975–90. The third and largest group comprised nine plots (four oligotrophic and five mesotrophic) in which most plants had established between 1940–70.

When examined individually, plots in groups 2 and 3 had strongly peaked bell-shaped age distributions with the majority of plants having established within 10–30 years of each other, followed by little subsequent regeneration. Such relatively even-aged cohorts imply establishment in a pulse following a disturbance or significant environmental change. The age of the oldest tree or shrub in each plot provides minimum dates for the disturbances or environmental events that initiated cohort establishment; these are plotted in Fig. 2c. Dates of cohort initiation were concentrated in the period 1930–80, but especially in the decade 1940–50, during which time grazing continued.

For plots in group 3, a peak in establishment occurs around 1970 with the subsequent drop-off in establishment coinciding with the removal of sheep grazing south of the fence constructed in 1970 (Fig. 3). However, this decline in establishment appears unrelated to grazing removal because plots in group 3 were located both north and south of the fenceline (Fig. 1), and all show the same pattern despite differences in their grazing history. Indeed, all three groups contain plots located both north and south of the 1970 fenceline, implying that factors other than variation in recent grazing history dominate establishment patterns. Instead of being related to grazing, the marked absence of recent regeneration in most plots probably results from low light levels caused by canopy closure as the relatively even-aged cohorts of both shrubs and tussocks mature. Permanent plots at mid elevations established in 1970 show a subsequent considerable thinning of seedlings initiated in the preceding decade (C. Meurk unpub. data).

Differences among the three groupings of plots primarily reflect differences in soil type, fertility and elevation. The three plots in group 1, comprising large, old *Dracophyllum*, were on sheltered (mostly south facing), mesotrophic sites at low elevation (range = 10–58 m, mean = 28 m), while plots in the remaining two groups were found at all elevations up to 245 m (group 2: range = 13–203 m, mean = 115 m; group 3: range = 15–245 m, mean = 91 m) and on a range of aspects. Plots in group 2 were predominantly on eutrophic soils while plots in group 3 were on a mix of mesotrophic and oligotrophic soils. The initial establishment of *Dracophyllum* in group 2 plots, on predominantly flushed, eutrophic soils, commenced about the same time as establishment in group 3 plots, on mesotrophic and oligotrophic soils, but the establishment peak in group 2 plots is delayed by 15–20 years.

Deviations from winter mean rainfall on Campbell Island (an index of relative dryness) for the period that climate data are available (1941–95) show little relationship to dates of *Dracophyllum* establishment (Fig. 2), except that colonisation of the wet, eutrophic sites in group 2, which peaked in the mid-1980s, occurs during the period of consistently low winter rainfall in the period 1970–90.

Discussion

Most *Dracophyllum* plants we aged on Campbell Island established after 1930, confirming photographic records that document a major expansion of scrub cover in the second half of the twentieth century (Wilmshurst *et al.*, 2004). Characteristic, narrow, bell-shaped age-distributions show that in most plots *Dracophyllum* plants established as a relatively even-aged cohort following some environmental perturbation. The majority of these cohorts were initiated shortly after the abandonment of farming and the cessation of regular burning on the island in 1931. Hence, our results are consistent with the hypothesis that recent *Dracophyllum* scrub expansion on Campbell Island is due to an abrupt change in the fire regime, with *Dracophyllum* plants most likely invading sites from which they were previously excluded by the repeated fires. We can conclusively dismiss the claim by Zotov (1965) that the *Dracophyllum* stands we see today were established during the farming regime, and that “with the cessation of fires, came virtually the end of any further invasion of *Dracophyllum* and other shrubs. They are now merely continuing to grow in stature”. However, Zotov was correct in stating that some of the *Dracophyllum* shrubs established in tussock grassland pre-dated the termination of the fires (see Fig. 2, Group 1). In lowland, sheltered sites that escaped fire, *Dracophyllum* established throughout the period of human occupation.

The timing and pattern of *Dracophyllum* establishment is generally inconsistent with the two other hypotheses advanced to account for the recent spread. There is no evidence that the removal of sheep grazing north of the fence in 1970 or south of the fence in 1984 had any consistent effect on *Dracophyllum* establishment: plots north and south of the fence behaved in a similar manner regardless of differences in grazing history.

Warming temperatures during the latter half of the twentieth century likewise do not seem to explain scrub spread. The Campbell Island climate record shows little trend in summer or winter temperatures from 1941 to 1975 (Salinger *et al.*, 1992; NIWA, 2003), and mean temperatures actually fell between 1957 and 1967 by about 1°C during the period of rapid *Dracophyllum* establishment (Wilmshurst *et al.*, 2004). Previous temperature trends are also unlikely to account for the expansion of scrub. Campbell Island temperatures are closely correlated with those of mainland stations in the southern South Island, but the record from Dunedin and Invercargill shows virtually static temperatures from 1920 through to 1953 (Salinger *et al.*, 1992). However, the later spread of *Dracophyllum* into the wet eutrophic sites coincides with a period of low winter rainfall (1970–1990) and is consistent with the photographic evidence for late spread onto poorly drained sites (Wilmshurst *et al.*, 2004). Whether this should be taken as evidence of any permanent change in the edaphic range of *Dracophyllum* on the island is not clear: it is possible that colonisation of wet sites has always depended on transient opportunities for establishment provided by a run of drier years.

The problem of why scrub was apparently restricted at the time of first European observations in 1840, and remained so until farming began in 1895, remains unsolved. Early sealer fires and wood gathering is likely to have impacted around the more heavily used areas, but for only a relatively brief period between 1810 and 1820. Episodic burning may have occurred after 1820, but was probably insufficient to repress *Dracophyllum* regrowth across large areas. It is possible that cooler, wetter climates during the 19th and early 20th century may have favoured tussock grassland (Wilmshurst *et al.* 2004) and that, once established, intact dense tussock cover excluded or restricted woody expansion for long periods. Therefore, at the time of European arrival, *Dracophyllum* could have been restricted by the dominance of tussocks and that the major loss of vegetation cover induced by farming, while repressing *Dracophyllum* regeneration, set the stage for its recovery once burning ceased.

Our results are pertinent to the interpretation of alpine forest and scrub change on the New Zealand mainland and elsewhere. Without the extensive documentary evidence for historical land-use changes on Campbell Island, it is highly probable that a major mid 20th century expansion of scrub at this remote treeline site would be regarded as unequivocal evidence for global warming. Alpine areas are often poorly documented, but rarely free from human interference. Cautious evaluation of the evidence is necessary before claims that global warming is driving expansions of woody vegetation at treeline are made.

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