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# High mountain bioclimate: temperatures near the ground recorded from the timberline to the nival zone in the Central Alps

**Walter Larcher & Johanna Wagner**

## ABSTRACT

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**In the Tyrolean Central Alps boundary layer temperatures of microsites were compared to free atmosphere temperatures between the timberline and the permanent snow-line. The microclimatic temperatures at the subalpine timberline (1950 m a.s.l.), in the upper-alpine vegetation belt (2200 m und 2230 m a.s.l.), and at a subnival (2880 m a.s.l.) and a nival (3450 m a.s.l.) site were continuously recorded using small data loggers.**

**During winter, the temperatures under the snow cover remained constant at 0°C or a few degrees below. Therefore, the lowest temperatures recorded by the weather service are not relevant to plants protected by snow, poikilothermic animals or microorganisms. It is the snow-free period that is bioclimatically relevant. In the years between 2000 and 2004 the snow-free period lasted 178 days at the timberline, about 90 to 110 days in the upper-alpine belt, 93 days at the subnival site and 74 days at the nival site.**

**During the snow-free period, the mean boundary layer temperatures were about 8°C at the timberline and in the upper-alpine belt on a southern slope, but only about 6°C on a northern slope. At the same time, the temperatures of the free air were 7°C at the timberline, and 6°C in the upper-alpine zone. Near the glacier, mean temperatures were 8.2°C at the subnival microsite and 3.6°C at the nival microsite (in contrast, the free atmosphere temperatures were 3.3°C and 1.6°C). In sheltered niches alpine plants heat up. Thus, the height gradient of their noon temperatures is gentler than the height gradient of the air temperature at 2 m. Under strong irradiation, prostrate plants, even in the glacier area, heat up to 25–30°C (which means overheating of up to 20 K above the air temperature at 2 m).**

**As the bioclimate is much more moderate than the severe macroclimate, alpine organisms can successfully develop and endure in the high mountains. Some examples of characteristic features of morphological and functional adaptations in high mountain plants are given.**

Keywords: Alpine macroclimate, microclimatic temperatures, snow-free period, freezing period, soil temperatures, altitudinal life zones, glacier foreland, mountain plants.

## Introduction

High mountains are extreme habitats that set selective limits to the altitudinal distributions of organisms (Franz 1979). The decrease of diversity and density of organisms mirror the poor quality of life. The elevational steps of vegetation reflect the boundaries of growth and the limited productivity of plants.

The climatic boundaries of high mountain regions are the timberline and the permanent snow-line (Troll 1966). With increasing elevation temperature decreases. Above the timberline the frequency and intensity of wind rises while the distribution of precipitation gets more uneven. The high mountain climate is defined by small-scale, terrain-dependent and short-term changeability. Sunny slopes and windy ridges are fairly dry and show rather little snow in winter whereas sheltered hollows are relatively wet in summer and permanently covered with snow during winter (Aulitzky 1963, Turner & al. 1975, Larcher 1985).

The bioclimate, which is the microclimate from the upper surface of the vegetation down to the deepest roots in the soil (Lowry 1967, Cernusca 1976) is more balanced, warmer and wetter than the surrounding air. The diversity of the habitats and the complexity of the bioclimate, however, make measurements more difficult. Therefore, no comprehensive results for the high mountain regions are available. In our contribution, representative examples of boundary temperatures in the habitat of plants, animals and microorganisms between timberline and glacier regions are presented and compared with the temperatures of the free air.

## Sites and Methods

### Study areas

In the Tyrolean Central Alps temperatures were recorded at the subalpine timberline and in the upper-alpine vegetation belt at Mt Patscherkofel (near Innsbruck, west of the Tux Alps) as well as at a subnival and a nival sites in the Stubai and Ötztal Alps.

On **Mt Patscherkofel** (47° 13’ N, 11° 20’ E) the timberline on the northern slope ranges from 1920 to 1950 m a.s.l. The alpine dwarf shrubs cover a 150 to 200 m elevational range from the *Rhododendro-Vaccinietum* to the open *Loiseleurio-Cetrarietum* shortly below the summit (2247 m). There on windy spots graminoids grow together with single dwarf shrubs and small rhododendrons. At the timberline, temperatures were recorded in a dense *Rhododendron* stand on a western slope (15° inclination). On the summit two temperature loggers were positioned: one on a southern slope (2200 m a.s.l., 25° inclination) and the other one on a northern slope (2230 m a.s.l., 35° inclination).

In the **Stubai Alps** only microclimatic temperatures were recorded at a subnival site in the glacier foreland of the Schaufelferner (2880 m a.s.l., 46° 59’ N, 11° 07’ E). The investigated microsite was a flat, rocky plateau (10° inclination, NNE) with scattered pioneer vegetation. The most frequent plant species were *Saxifraga bryoides*, *Cerastium uniflorum* and *Ranunculus glacialis*, accompanied by a few cushions of *Saxifraga exarata* and *Androsace alpina*.

The highest site was on Mt Brunnenkogel in the **Ötztal Alps** (3450 m a.s.l., 46° 55’N, 10° 52’E). This mountain rises like a nunatak from the Pitztal glacier area and is fully glaciated on the northern side. A small crest on the top and the nearly vertical southern flank are ice free. Temperature measurements were carried out on a small plateau at the crest with typical elements of a nival plant association consisting of *Saxifraga bryoides*, *Cerastium uniflorum*, *Ranunculus glacialis*, *Leucanthemopsis alpina* and *Poa laxa*.

## Method

Microclimate temperatures were continuously recorded at hourly intervals using small data loggers of 3 cm diameter and 1.2 cm height ("StowAway Tidbit", Onset Computer Corp. Pocasset MA, USA). The loggers have a NTC-pearl sensor and were protected from direct radiation. Loggers at Mt Patscherkofel were installed on rhododendron twigs or buried at a depth of 10 cm. At the subnival and the nival site with open vegetation, loggers were placed in plant cushions so that the sensors were shaded by leaves. Temperature data also indicated the duration of snow cover at the different sites.

Temperature data of the free atmosphere were provided by the surrounding meteorological stations of the official weather service.

## Results

### Air temperatures between timberline and permanent snow-line

In the Central Alps the temperatures of the free atmosphere are reduced according to the adiabatic lapse rate by on average 0.65°C per 100 m during summer (Kuhn 1997). The linear gradient of the mean annual air temperature measured between 1950 m and 3440 m a.s.l. by the meteorological stations in our investigation area is 0.58°C per 100 m. The mean July temperature gradient is 0.56°C per 100 m.

The Tabs. 1 and 2 show long-term air temperature measurements of the weather stations for the mountain climate between the timberline and the summit of Mt Patscherkofel. Tabs. 3 and 4 show temperature data of more recent measurements carried out over several years by the weather services in the glacier areas of the Ötztal Alps (glacier foreland of Mittelbergferner 2850 m, and Mt Brunnenkogel 3440 m a.s.l.).

At the timberline on Mt Patscherkofel the annual mean air temperature at 2 m height was 2.1°C, on Mittelbergferner –2.4°C and on Mt Brunnenkogel –6.5°C. Mean temperatures during summer (June until the end of August) were 8.8°C at the subalpine timberline, 7.2°C in the 300 m higher upper-alpine belt, 4.9°C at the subnival site in the glacier foreland and only 0,9°C on the nival summit. The current climate change brings about exceptionally warm years: In 2002, the annual mean temperatures at the timberline was 3.7°C; in the year 2003, which was characterised by strong solar irradiation and unusually long warm periods, the annual mean temperature was 4.1°C. On the Mittelbergferner the annual mean temperature was –1.8°C in 2002 and –1.7°C in 2003.

During winter, absolute minima of the air temperature, –28°C to –31°C, are similar in all altitudinal belts. During midsummer (July to August) freezing temperatures from –5°C at the timberline to –7°C and –10°C in the glacier area can occur. Long-term measurements at the timberline showed 183 days of the year with minimum air temperature ≤ 0°C and 90 days with a maximum temperature ≤ 0°C. On the summit of Mt Patscherkofel measurements resulted in 223 days with minimum air temperature ≤ 0°C and 137 days with a maximum temperature ≤ 0°C. In the glacier area the length of the freezing period is considerably longer, namely 274 to 324 days with minimum air temperature ≤ 0°C and 160 to 237 days with a maximum temperature ≤ 0°C. However, most high mountain organisms are hardly affected by these low temperatures as they are protected by a layer of snow. Only several pioneer plants (cushion plants,

| 1963–1992 | Tm [°C ] | Tm max [°C] | Tm min [°C] | Max abs [°C] | Min abs [°C] | Days min ≤ 0°C | Days max ≤ 0°C |
|---|---|---|---|---|---|---|---|
| January | −4.6 | 4.7 | −13.5 | 11.0 | −28.0 | 29.3 | 19.2 |
| February | −4.9 | 5.6 | −13.2 | 14.4 | −22.4 | 27.3 | 17.1 |
| March | −2.7 | 6.8 | −9.1 | 16.0 | −16.2 | 26.3 | 13.8 |
| April | −0.7 | 8.8 | −8.7 | 15.9 | −18.0 | 22.0 | 9.1 |
| May | 4.2 | 14.8 | −4.9 | 21.0 | −11.9 | 11.0 | 1.4 |
| June | 7.3 | 15.4 | −1.4 | 22.0 | −4.8 | 4.1 | 0.3 |
| July | 9.7 | 16.6 | 0.6 | 26.0 | −5.2 | 1.0 | 0.3 |
| August | 9.5 | 17.0 | 0.3 | 25.1 | −4.9 | 1.1 | 0.0 |
| September | 7.2 | 14.3 | −1.1 | 21.6 | −4.8 | 3.4 | 0.1 |
| October | 4.0 | 13.3 | −5.5 | 18.6 | −14.8 | 10.5 | 3.1 |
| November | −0.7 | 10.4 | −11.2 | 15.0 | −18.2 | 20.3 | 9.5 |
| December | −3.1 | 7.0 | −12.8 | 13.5 | −20.5 | 27.0 | 15.6 |
| **Year** | **2.1** | | | | | **183.3** | **89.7** |
| *Extreme* | | *17.0* | *−13.5* | *26.0* | *−28.0* | | |

**Tab. 1. Long-term air temperature at 2 m height at the timberline of Mt Patscherkofel (1950 m a.s.l.) provided by the Federal Office and Research Centre for Forests (Innsbruck). Tm = mean air temperature; Tm max = monthly mean of the daily maxima; Tm min = monthly mean of the daily minima; Max abs = absolute maximum; Min abs = absolute minimum; Days min ≤ 0°C = number of days with minimum at 0°C or subzero temperature; Days max ≤ 0°C = number of days with maximum at 0°C or subzero temperature.**

| 1961–1990 | Tm [°C ] | Tm max [°C] | Tm min [°C] | Max abs [°C] | Min abs [°C] | Days min ≤ 0°C | Days max ≤ 0°C |
|---|---|---|---|---|---|---|---|
| January | −6.7 | 3.3 | −17.9 | 9.5 | −29.5 | 30.8 | 25.5 |
| February | −6.9 | 3.0 | −16.6 | 9.5 | −25.6 | 27.7 | 23.7 |
| March | −5.2 | 4.6 | −15.5 | 8.2 | −26.3 | 29.6 | 22.2 |
| April | −2.5 | 6.8 | −11.9 | 12.8 | −16.3 | 26.3 | 15.3 |
| May | 2.0 | 12.3 | −7.5 | 17.2 | −13.6 | 17.8 | 5.1 |
| June | 5.6 | 16.4 | −3.8 | 21.2 | −6.7 | 8.2 | 1.7 |
| July | 8.1 | 18.3 | −1.5 | 23.4 | −3.7 | 3.5 | 0.4 |
| August | 8.0 | 18.1 | −1.5 | 21.6 | −3.6 | 3.3 | 0.3 |
| September | 6.0 | 15.7 | −3.5 | 21.3 | −7.7 | 7.5 | 1.7 |
| October | 2.8 | 12.5 | −7.5 | 16.3 | −12.7 | 14.1 | 4.5 |
| November | −2.6 | 8.3 | −13.9 | 12.2 | −20.4 | 25.0 | 14.5 |
| December | −5.4 | 5.2 | −17.1 | 9.8 | −22.7 | 29.5 | 21.8 |
| **Year** | **0.2** | | | | | **223** | **137** |
| *Extreme* | | *18.3* | *−17.9* | *23.4* | *−29.5* | | |

**Tab. 2. Long-term air temperature at 2 m height at the summit of Mt Patscherkofel (2247 m a.s.l.) provided by the Central Institute for Meteorology and Geodynamics, Regional Center for the Tyrol and Vorarlberg. Tm = mean air temperature; Tm max = monthly mean of the daily maxima; Tm min = monthly mean of the daily minima; Max abs = absolute maximum; Min abs = absolute minimum; Days min ≤ 0°C = number of days with minimum at 0°C or subzero temperature; Days max ≤ 0°C = number of days with maximum at 0°C or subzero temperature.**

| 1995–2005 | Tm [°C ] | Tm max [°C] | Tm min [°C] | Max abs [°C] | Min abs [°C] | Days min ≤ 0°C | Days max ≤ 0°C |
|---|---|---|---|---|---|---|---|
| January | −8.9 | −5.6 | −12.1 | 5.8 | −27.0 | 31.0 | 27.8 |
| February | −9.4 | −5.9 | −12.9 | 6.9 | −29.0 | 28.3 | 24.4 |
| March | −7.6 | −4.3 | −10.9 | 6.8 | −26.3 | 31.0 | 24.0 |
| April | −5.5 | −2.1 | −8.8 | 7.5 | −23.4 | 30.2 | 20.7 |
| May | 0.3 | 3.5 | −3.0 | 13.0 | −14.7 | 23.8 | 5.2 |
| June | 3.6 | 7.0 | 0.3 | 15.4 | −14.0 | 14.8 | 2.5 |
| July | 5.2 | 8.6 | 1.9 | 17.6 | −7.0 | 9.0 | 0.8 |
| August | 5.9 | 9.0 | 2.7 | 17.5 | −7.3 | 5.5 | 0.5 |
| September | 2.0 | 5.1 | −1.2 | 15.1 | −11.4 | 17.2 | 4.1 |
| October | 0.1 | 3.1 | −3.0 | 12.6 | −19.4 | 22.5 | 6.0 |
| November | −6.0 | −2.6 | −8.2 | 9.5 | −23.0 | 29.5 | 20.6 |
| December | −8.0 | −4.4 | −10.1 | 5.3 | −26.3 | 31.0 | 23.1 |
| **Year** | **−2.4** | | | | | **274** | **160** |
| *Extreme* | | *9.0* | *−12.9* | *17.6* | *−29.0* | | |

**Tab. 3. Air temperature at 2 m height at the Mittelbergferner (Ötztal Alps 2850 m a.s.l.) provided by the Central Institute for Meteorology and Geodynamics, Regional Center for the Tyrol and Vorarlberg. Tm = mean air temperature; Tm max = monthly mean of the daily maxima; Tm min = monthly mean of the daily minima; Max abs = absolute maximum; Min abs = absolute minimum; Days min ≤ 0°C = number of days with minimum at 0°C or subzero temperature; Days max ≤ 0°C = number of days with maximum at 0°C or subzero temperature.**

| 2003–2005* | Tm [°C ] | Tm max [°C] | Tm min [°C] | Max abs [°C] | Min abs [°C] | Days min ≤ 0°C | Days max ≤ 0°C |
|---|---|---|---|---|---|---|---|
| January | −14.9 | −11.9 | −18.0 | 0.0 | −29.1 | 31.0 | 31.0 |
| February | −15.6 | −13.0 | −18.3 | 1.0 | −30.8 | 28.5 | 28.0 |
| March | −12.0 | −9.4 | −14.5 | 1.7 | −27.8 | 31.0 | 30.0 |
| April | −8.8 | −6.0 | −11.6 | 0.9 | −20.0 | 30.5 | 29.5 |
| May | −5.2 | −2.2 | −8.1 | 8.8 | −18.6 | 28.5 | 22.0 |
| June | −0.9 | 2.2 | −3.9 | 11.0 | −14.7 | 23.5 | 10.0 |
| July | 1.3 | 4.4 | −1.8 | 12.3 | −9.0 | 20.7 | 4.0 |
| August | 1.9 | 4.9 | −1.0 | 12.7 | −10.5 | 18.3 | 3.0 |
| September | −0.3 | 2.7 | −3.4 | 10.3 | −11.9 | 22.7 | 8.7 |
| October | −3.7 | −1.1 | −6.2 | 8.7 | −22.2 | 28.3 | 16.3 |
| November | −8.7 | −3.6 | −14.2 | 1.8 | −20.8 | 30.0 | 23.7 |
| December | −11.7 | −7.4 | −16.6 | −0.8 | −26.2 | 31.0 | 30.7 |
| **Year** | **−6.5** | | | | | **324** | **237** |
| *Extreme* | | *4.9* | *−18.3* | *12.7* | *−30.8* | | |

* in operation since 2003

**Tab. 4. Air temperature at 2 m height at the summit of Mt Brunnenkogel (Ötztal Alps 3440 m a.s.l.) provided by the Central Institute for Meteorology and Geodynamics, Regional Center for the Tyrol and Vorarlberg. Tm = mean air temperature; Tm max = monthly mean of the daily maxima; Tm min = monthly mean of the daily minima; Max abs = absolute maximum; Min abs = absolute minimum; Days min ≤ 0°C = number of days with minimum at 0°C or subzero temperature; Days max ≤ 0°C = number of days with maximum at 0°C or subzero temperature.**

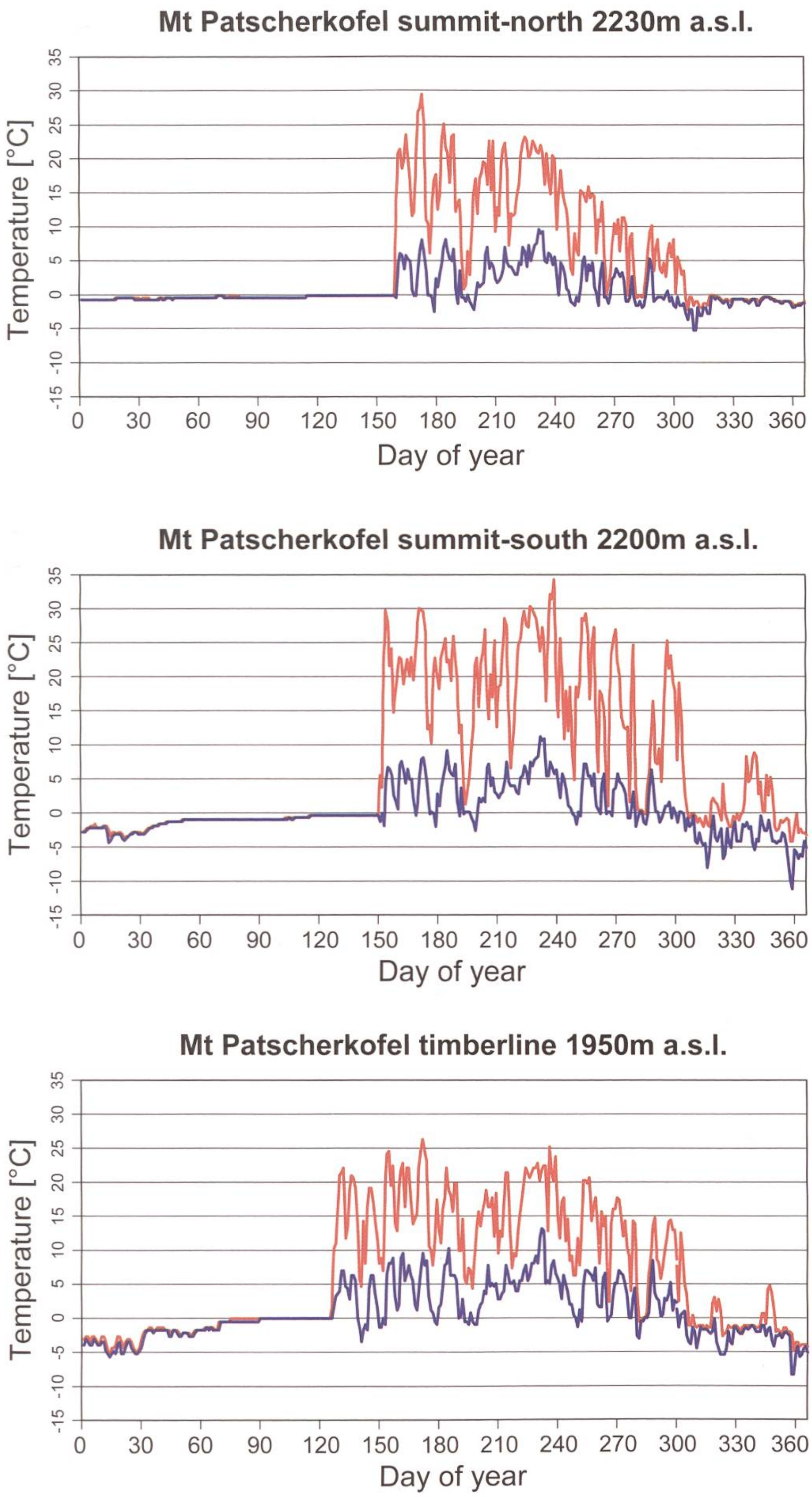


**Fig. 1. The annual variation of shrub temperatures of *Rhododendron ferrugineum* on Mt Patscherkofel during the climatically normal year 2000. Lower graph: subalpine site at the timberline. Middle graph: upper alpine site on the southern slope of the summit. Upper graph: site on the northern slope of the summit. Red line: daily maximum, black line: daily minimum.**

mosses and lichens) and alpine graminoides on snow-free and windy ridges are exposed to much lower temperatures just like some arthropods, birds and certain mammals.

## Microclimatic temperatures of the investigated habitats

The annual course of temperature at the microsites in the four altitudinal belts is shown in Figs. 1 and 2. The graphics demonstrate data series from 2000 (Mt Patscherkofel sites) and 2004 (glacier sites) as an example for climatically normal years.

At the timberline of Mt Patscherkofel temperatures were monitored in a 30–50 cm high stand of *R. ferrugineum*. On the summit, crown temperatures were measured in isolated dwarf shrubs and soil temperature was recorded at a depth of 10 cm (Fig. 1). During winter, temperature conditions under the snow cover are balanced (between 0°C and not lower than –5°C). However, a continuous snow cover is unfavourable to the activity and development of the organisms. It is therefore convenient to use the *snow-free period* – the period between melting in spring to snow coverage in late autumn – as a reference for bioclimatic investigations (Friedel 1961; Turner 1961). In the year 2000 on Mt Patscherkofel the snow started to melt at the timberline at the beginning of May, on the southern slope of the summit at the end of May, and on the northern slope from mid-June onwards; in this year the snow-free period ranged from 178 days (at the timberline) to 145 days (northern slope of the summit) until a closed snow cover formed again at the beginning of November (Tab. 5). In the Austrian Central Alps there is an average snow cover in winter for 127 days at 1000 m a.s.l., 167 days at 1500 m a.s.l. and 214 days at 2000 m a.s.l. (Lauscher & Lauscher 1980).

During the snow-free period, mean boundary layer temperature at the timberline as well as on the southern slope of the summit reached approximately 8°C; the northern slope only approximately 6°C (Tab. 6). At the timberline and on the southern slope of the summit temperatures between 5 and 10°C were most common, namely 39% or 31% of hours during the measuring period (Fig. 3); on the northern slope, however, lower temperatures of 0–5°C were

| Sites | Altitude | Beginning of snow-free period | End of snow-free period | Length of snow-free period [d] | Days with ≤ 0°C | Days with > 0°C |
|---|---|---|---|---|---|---|
| **Nival zone** | 3450 m | 27. 06. 2004 | 09. 09. 2004 | **74** | 51 | 23 |
| **Subnival zone** | 2880 m | 24. 06. 2004 | 25. 09. 2004 | **93** | 18 | 75 |
| **Upper-alpine north** | 2230 m | 08. 06. 2000 | 31. 10. 2000 | **145** | 52 | 93 |
| **Upper-alpine south** | 2200 m | 30. 05. 2000 | 31. 10. 2000 | **154** | 32 | 112 |
| **Timberline** | 1950 m | 06. 05. 2000 | 31. 10. 2000 | **178** | 35 | 143 |

**Tab. 5. Number of days with freezing and frost-free temperatures during the snow-free period.**

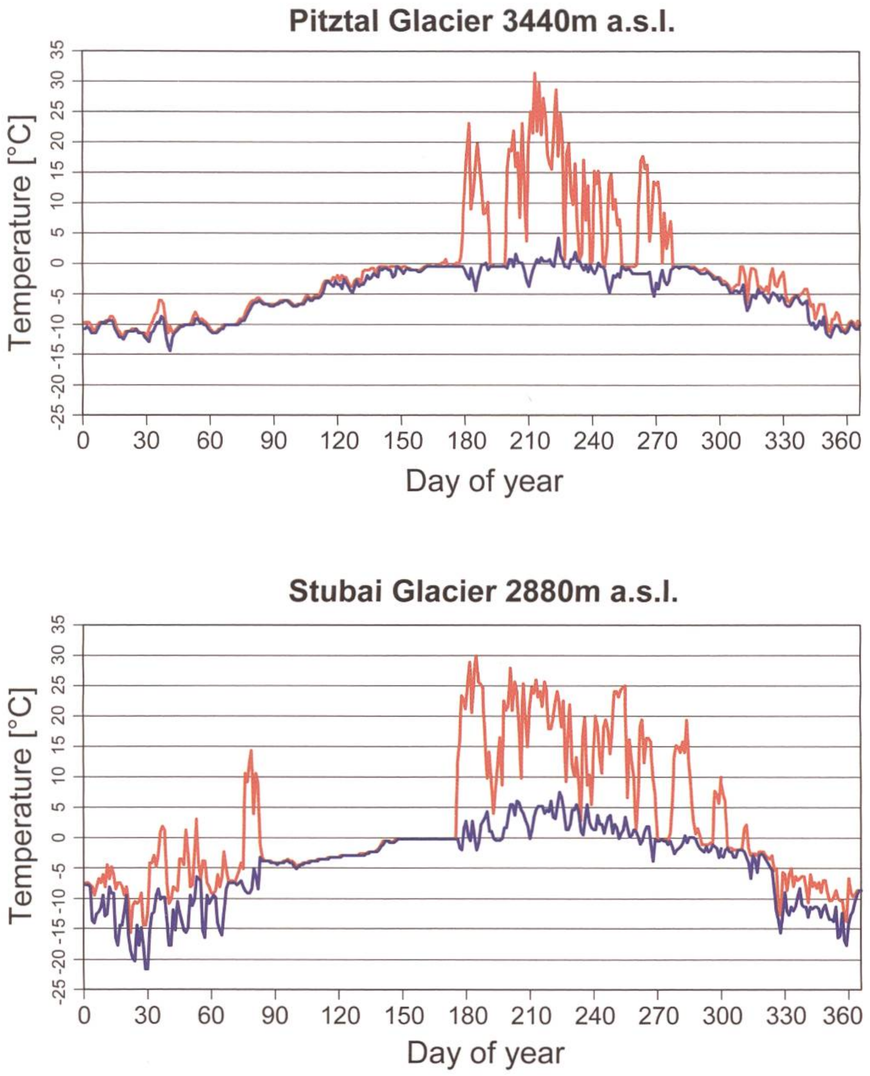


**Fig. 2. The annual variation of boundary layer temperatures in the glacier regions during the climatically normal year 2004. Lower graph: subnival site in the glacier foreland of the Schaufelferner in the Stubai Alps. Logger situated in cushion plant (*Saxifraga bryoides*). Upper graph: subnival site on Mt Brunnenkogel in the Ötztal Alps. Logger placed under full canopy shade. Red line: daily maximum, blue line: daily minimum.**

most frequent (31%). During the night temperatures between 0 and 5°C (42% of all hours) and 5–10°C (38%) were most often measured on the southern slope of the summit. During daylight hours the range of the frequency distribution was much broader, namely 0 to 20°C (Fig. 4). At the beginning of the snow-free period (May–June) there were 32 to 52 days with minimum air tem-

| Sites | Altitude | Temp sf* [°C] | Most frequent Temp. range** [%] | Max abs [°C] | Min abs [°C] |
|---|---|---|---|---|---|
| **Nival zone** | 3450 m | **3.6** | 0–5°C (43%) | 31.4 (July) | –4.5 (July) |
| **Subnival zone** | 2880 m | **8.2** | 0–5°C (33%) | 29.9 (July) | –3.9 (Sept) |
| **Upper-alpine north** | 2230 m | **6.4** | 0–5°C (31%) | 29.4 (June) | –2.5 (June) |
| **Upper-alpine south** | 2200 m | **8.5** | 5–10°C (31%) | 34.3 (Aug) | –2.7 (July) |
| **Timberline** | 1950 m | **8.1** | 5–10°C (39%) | 26.3 (June) | –3.5 (May) |

* Temp sf = mean plant temperatures during the snow–free period

** Most frequent temperature range in percent of hours during the snow–free period

**Tab. 6. Characteristics of the investigated sites during the snow-free period.**

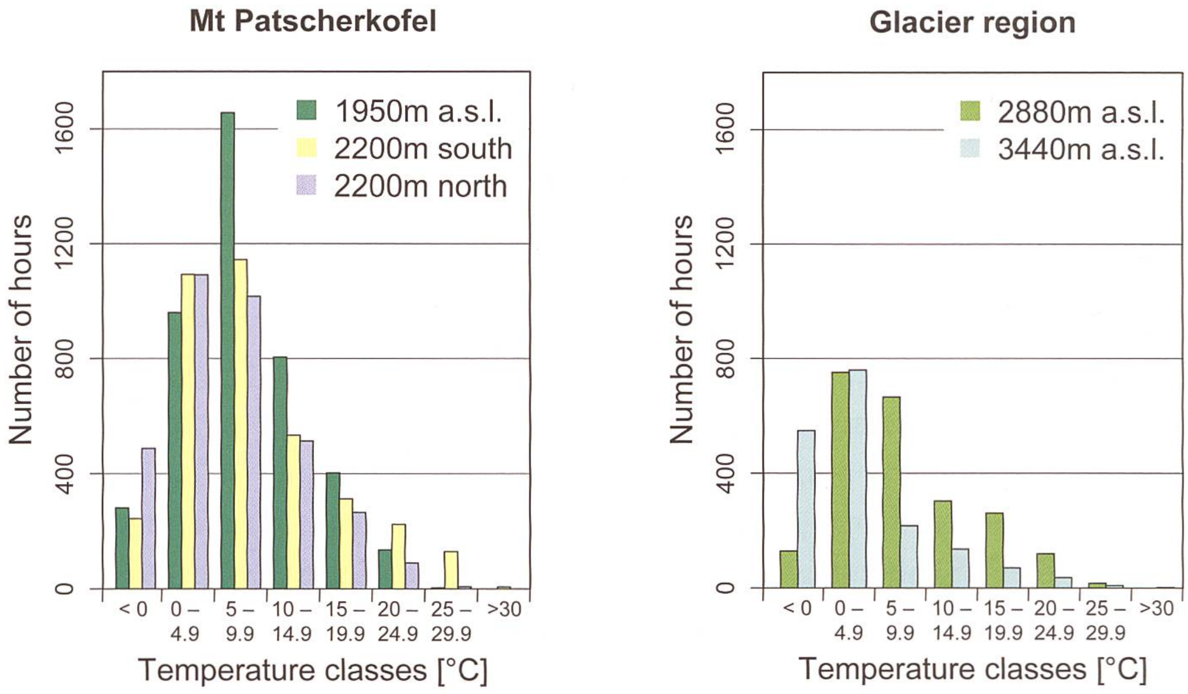


**Fig. 3. Frequency of the number of hours during the snow-free period in different temperature classes and sites on Mt Patscherkofel and in the glacier regions.**

peratures from –2.5 to –3.5°C. So, 143 days at the timberline, 112 days on the southern slope of the summit and 93 days on the northern slope of the summit were frost-free. The monthly means of the daily maxima were 14°C (July) and 18°C (August) at the timberline, 17 and 24°C on the southern slope of the summit and 15 and 18°C on the northern slope of the summit. High temperatures of above 25°C were only reached in this year on the southern slope of the summit (138 hours). On summer days with strong incoming radiation, absolute leaf temperature maxima of 40–42°C can occur in the alpine dwarf-shrub community (Cernusca 1976, Larcher & Wagner 1976).

In the glacier regions temperatures were measured on the Schaufelferner (2880 m a.s.l.) in the Stubai Alps at a windy and flat microsite with little snow cover in winter. At the highest investigation site (Mt Brunnenkogel, 3450 m a.s.l.) in the Ötztal Alps, temperatures were recorded on the sheltered soil surface by placing the loggers between rosettes of *R. glacialis* (Fig. 2). During winter, temperatures under the permanent snow cover fell to –10°C at 2880 m a.s.l. and to –15°C at 3450 m a.s.l. At microsites open to steep slopes or snow-free spots, which are very often covered with cushion plants, temperatures of up to –25°C can occur. At both localities the snow melted between the end of June and the beginning of July in 2004. In autumn a closed snow cover formed at the beginning of September (Mt. Brunnenkogel) or at the end of September (Schaufelferner). Thus, the duration of the snow-free period was 93 days at the subnival site and 74 days on the summit of Mt Brunnenkogel (Tab. 5).

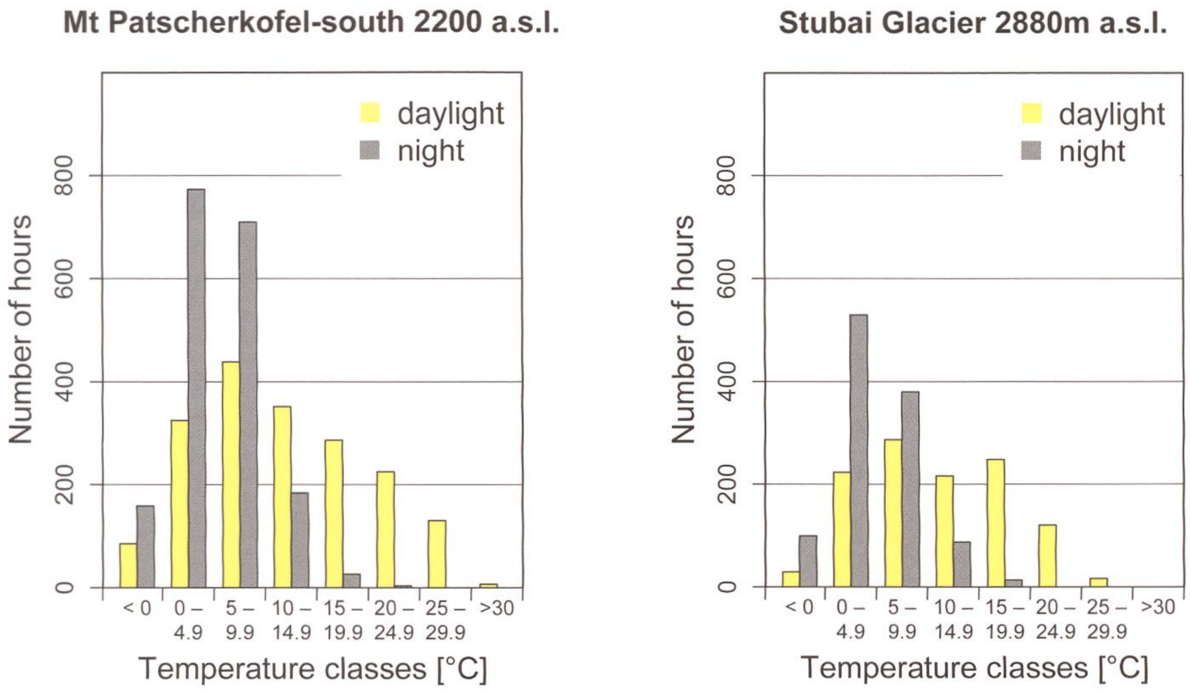


**Fig. 4. Frequency of the daylight and night hours during the snow-free period in different temperature classes and sites on the southern slope of Mt Patscherkofel (2200 m a.s.l.) and in the glacier foreland of the Schaufelferner (2880 m a.s.l.).**

After snowmelt the sun was in the zenith and consequently high noon boundary layer temperatures were measured. From mid-August onwards the temperatures continually fell. All in all, boundary layer temperatures were 8.2°C at 2880 m a.s.l. and 3.6°C at 3450 m a.s.l. (Tab. 6). After snowmelt from July until mid-August maximum daily means around 20–25°C were measured at both investigation sites; minimum daily means were 2 to 5°C but there also occurred temperatures of around 0°C several times.

Remarkable is the difference between the subnival and nival zone in the frequency distribution of the number of hours for the respective temperature ranges (Fig. 3): during the snow-free period 33% of hours were between 0 and 5°C on the Schaufelferner, but 43% on Mt Brunnenkogel. Furthermore on Mt Brunnenkogel, 31% of all hours showed temperatures of less than 0°C. At the investigation site at 2880 m a.s.l. almost half of the night hours are in the temperature range 0–5°C whereas the daylight hours distribute with about 20–25% over all four temperature ranges between 0 and 20°C (Fig. 4).

During the snow-free period there were 18 days with minimum temperature ≤ 0°C and 75 days without any frost on the Schaufelferner; on Mt Brunnenkofel there were 51 days with minimum temperature ≤ 0°C of which 10 were days with a maximum temperature ≤ 0°C and 23 were days without frost. Negative temperatures of below 0°C (absolute minimum –4 to –4.5°C) were measured in 6% of all hours on the Schaufelferner and in 31% of all hours on Mt Brunnenkogel. That means that on nival mountain summits – in contrast to

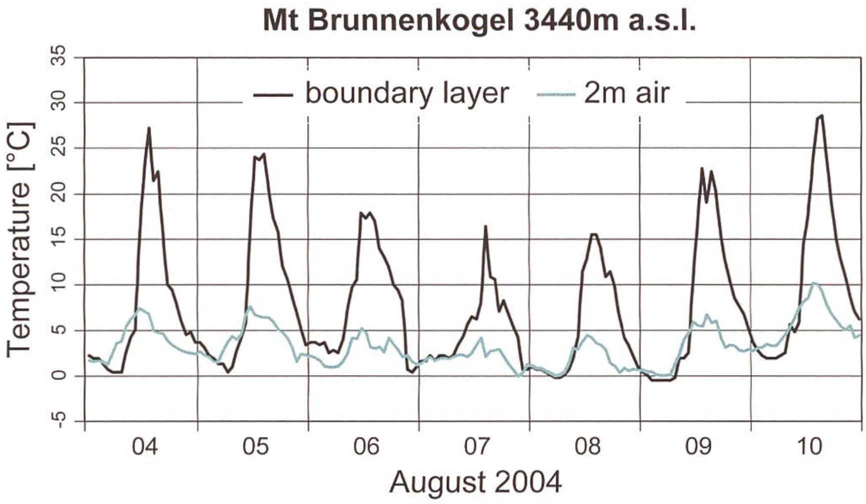


**Fig. 5.** Diurnal course of the boundary layer temperatures on soil surface (in shade) and air temperature at 2m height on Mt Brunnenkogel from 4th to 10th August 2004.

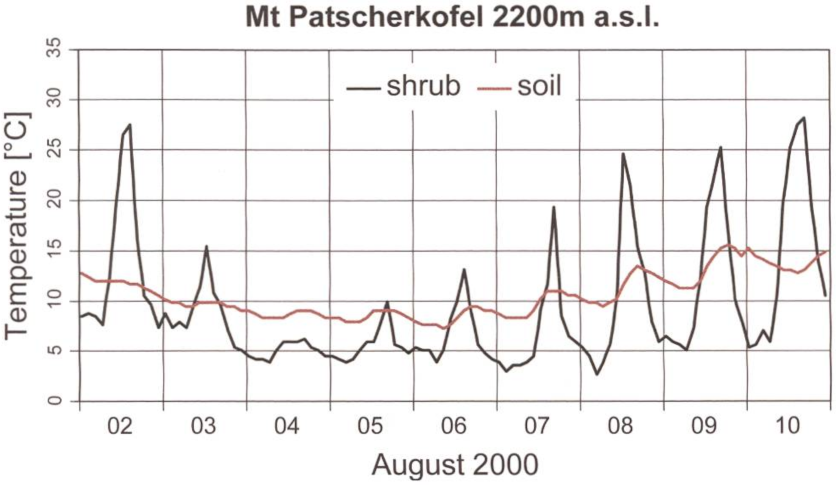
the subnival belt – the boundary layer temperatures frequently fall below 0°C during the night in summer. Maximum daily means of about 19°C were calculated for the Schaufelferner and 12°C for Mt Brunnenkogel. In certain microhabitats on the highest summits in the Alps temperatures of up to 30°C can occur during certain hours on a clear day.

## Discussion

At the various microsites in the high mountains temperatures do not only change horizontally over a short distance but also vertically (Moser & al. 1977, Kuhn 1997). Extensive temperatures differences between the free atmosphere and the boundary layer climate can occur. Also below the surface down to a depth of 50 cm there are significant temperature changes in time and quantity (Eckel 1960). A large amount of the absorbed solar radiation is saved in form of warmth by the plants. In case of sparse vegetation the heat is passed on into deeper layers of the soil. In sheltered niches alpine plants heat up more than lowland plants so that their elevational gradient of noon temperatures is gentler than the adiabatic lapse rate of the air temperature at 2 m (Wilson & al. 1987, Körner 2003). In our investigations of the bioclimate between 1950 m and 3440 m we found a linear temperature gradient of 0.4–0.5°C per 100 m.

In dwarf vegetation, temperatures due to strong irradiation may differ by 10–15 K [temperatures are presented in K, as differences of degrees centigrade] between sunrise (minimum temperature) and early afternoon (maximum temperature). Similarly rosette plants and cushion plants in the glacier area heat up to 25–30°C under strong irradiation, which means overheating up to 20 K above the air temperature at 2 m (Fig. 5). Due to wind and clouds, boundary layer temperatures can take on the temperatures of the free air. On clear

**Fig. 6. Diurnal temperature course in the crown of *Rhododendron ferrugineum* and soil temperatures at 10 cm depth on the southern slope of Mt Patscherkofel from 2nd to 10th August 2000.**



nights lower temperatures can occur in the morning because of emitted thermal re-radiation.

The soil buffers the heat balance of a habitat by taking up a considerable quantity of heat during the day and by releasing it again at night. In contrast to the boundary layer temperatures with a very high amplitude, soil temperature varies only slightly. Furthermore, changes in the soil temperature are delayed in time compared to the air temperatures. The daily fluctuations during the summer lie between 5 and 10°C (Fig. 6). All in all, soil temperatures in the root environment on the southern slope of the summit of Mt Patscherkofel amounted to about 10°C during the warmest month and about 8°C from June to September.

From temperature records over several years in the glacier region at 3184 m a.s.l. in the Stubai Alps (Mt Hoher Nebelkogel; Moser & al. 1977) it is known that only for about 3 months the soil temperature at 10 cm depth is above the subzero temperature range. At a ridge site during the warmest month (July) an average soil temperature of 2.8°C was measured. The mean maximum temperature amounted to 6.1°C and the mean minimum temperature to 0.2°C. On single sunny days the soil temperature could range from zero in the morning to 6°C in the afternoon. During clear summer days the surface temperature on rocks at the Jungfraujoch (3700 m a.s.l., Swiss Alps) ranges from –1 to –2°C in the morning to 32–35°C at noon (Mathys 1974). Inside the rocks at a depth of 10 cm temperature amplitudes of 0 to 5°C (minimum) and 24–28°C (maximum) occur; at a depth of 20 cm the temperature ranges between 3–8°C to 20–22°C and at a depth of 40 cm only between 5–9 ° and 10–14°C.

This high variability of thermal mountain climate affects plants and animals in several ways. Cool summers and long winters reduce the growing season for plants and the activity period for animals. With increasing altitude there is a reduction in biomass, and in the numbers of species and individuals (Grabherr & al. 1995, Körner 2003). Species adapted to high altitudes are smaller, and are more resistant to disturbances. Vascular mountain plants of high elevations are small, mostly perennial rosette and cushion plants, graminoids, and dwarf shrubs (Körner & Larcher 1988, Körner & al. 1989). Prostrate plants are sheltered from the wind and covered with snow during the winter. In the Alps the soil surface temperatures under a cover of snow of more than 50 cm remain constant between 0 and –5°C (Sakai & Larcher 1987). Therefore, the lowest temperatures measured above the timberline by the weather services are bioclimatically not relevant for the vegetation and small animals.

Growth forms that profit from warmth like procumbent plants are thermally favoured. However, they are exposed to large short-term temperature changes during the snow-free period. Many alpine plants show an enormous flexibility in their metabolic processes; e.g. a broad temperature optimum for photosynthesis and a quick response of respiratory activity (Larcher 1980). In the case of sunny weather with considerable warming at noon photosynthesis and respiration can adapt within hours. Species of the alpine Ericacean heath assimilate $CO_2$ optimally between 14 and 30°C (Grabherr 1977, Larcher 1977), herbaceous species of the alpine grassland between 15 and 28°C (Körner & Diemer 1987). In the alpine belt a third of all daylight hours are in the optimal temperature range for photosynthesis; half are in the suboptimal range (from 10 to 32°C).

High mountain plants of the subnival and nival regions show an adaptive functionality of metabolic processes under low temperatures. At 5°C vascular plants of the high mountains assimilate 50–80%, and at 0°C 30–50% of the quantity of $CO_2$ that they can bind under optimal temperatures. In the case of rosette plants the temperature optimum of photosynthesis lies at 14–25 °C (e.g. *Ranunculus glacialis, Geum reptans* und *Oxyria digyna*; Körner & Diemer 1987), in the case of cushion plants at 10–15°C (e.g. *Saxifraga bryoides, S. moschata und S. oppositifolia;* Moser & al. 1977). Consequently, between 20% (cushion plants) and 32% (rosette plants) of the daylight hours lie in the optimal temperature range of photosynthesis and up to 44% of daylight hours are in the suboptimal range (5–15°C). Sufficient heat is a basic prerequisite for plant growth. In *Poa alpina* leaf extension growth ceases, when photosynthesis still occurs at 35% of its maximum (Körner & Woodward 1987). At 3000 m altitude, this grass grows mainly during warm daylight hours; in contrast, low-altitude grasses were found to grow day and night.

Temperatures not only affect the actual growth activity but the whole course of development. At the time of snowmelt plants shift from the dormant to the active state and have to pass the vegetative and reproductive growth cycle within a short period of time. Depending on relief and snow accumulation in winter, the snow-free period in mountains of the temperate zone lasts 3–5 months in the alpine belt, and 1–3 months in the nival belt.

Short growing seasons together with low temperatures particularly impair reproductive growth. At the timberline and in the alpine dwarf shrub belt, woody plants can fail to mature seeds because of thermal limitations (Larcher & Wagner 2004). Herbaceous plant species usually are not temperature limited at this elevation, except for late flowering species as *Gentianella germanica* (Wagner & Mitterhofer 1998) and individuals growing in late-thawing hollows (Ladinig & Wagner 2005, Larl & Wagner 2006). In the nival zone, however, where low temperatures occur more often, the different developmental phases are prolonged. Particularly the length of the prefloration period (i.e. the period between snowmelt and anthesis, during which the flower bud differentiation is completed and the flowering stems elongate) and histogenesis (i.e. the period of seed growth) correlate with temperature. In *Ranunculus glacialis* (nival species with the most rapid development), the prefloration period varies between 13 and 30 days and the period of seed development between 30 and 40 days depending on the frequency of hours below 2°C (unpublished results). In contrast, seed maturation in an advanced state seems to be rather insensitive to low temperatures and in several species continues even under the snow.

Mountain plants are endangered by temperature extremes which in most cases are harmful frosts and very seldom is short-term heat. Cushion plants, tussocks and dwarf shrubs on wind-exposed ridges survive low temperatures in winter because of highest frost tolerance. With full hardening alpine Ericaceae are resistant to –35 to –60°C, cushion plants like *Carex firma* and *Silene acaulis* are resistant to –70°C or even lower temperatures. For species that only survive under snow protection, like most rosette plants, frost resistance of –20 to –25°C is sufficient (Sakai & Larcher 1987). During the snow-free period alpine plants are under much greater risk of frost, especially when they are actively growing. Most herbaceous plant species are sensitive and are frozen at temperatures of about –4 to –8°C, only graminoids are hardier to about –8 to –11°C (Larcher & Wagner 1976, Taschler & Neuner 2004). After frost in spring in the alpine zone and in mid-summer in the glacier regions partially damaged leaves and flowers can be observed.

Adaptated mountain animals, together with plants, have advanced to the highest altitudes. Above the closed alpine vegetation, food is limited and topsoil becomes increasingly shallow and patchy. Animal life concentrates near the soil surface, The high mountain zone is inhabited by small invertebrates that depend on plants and their detritus. They colonize the upper humus layer or crevices (Meyer & Thaler 1995, Thaler 1999, 2003). Animals choose their most favourable bioclimate. With increasing elevation and decreasing temperatures, poikilothermic animals can only survive in their micro-environments because of irradiation heating of the soil surface and the boundary layer near the ground. Pollinating insects closely depend on higher plants whose flowers offer them food and shelter. Conversely, most high mountain plants depend on pollinators as they are preferably outbreeding. Low temperatures at higher altitudes cause lower visiting rates which are compensated for by prolonged anthesis of individual flowers (Arroyo & al. 1981, Bingham & Orthner 1998, Fabbro & Körner 2004). A longer period of stigma receptivity again increases the probability of insect pollination in the stochastic mountain climate (Steinacher & Wagner 2006).

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