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ORIGINAL PAPER

# Coldest places on earth with angiosperm plant life

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**Abstract** The highest elevation flowering plant ever recorded in Europe, a lush moss flora, one of the coldest places of permanent animal life (collembola, mites) and indications of mycorrhizal fungi were evidenced for the Dom summit (4,545 m, central Swiss Alps) between solid siliceous rock at 4,505–4,543 m, 46° N. Cushions of *Saxifraga oppositifolia* were found at 4,505 to 4,507 m a.s.l. A large individual (possibly >30 years old) was in full bloom on 12 August 2009. The <sup>14</sup>C-dated oldest debris of the biggest moss, *Tortula ruralis*, suggests a 13 year litter turnover. The thermal conditions at this outpost of plant life were assessed with a miniature data logger. The 2008/09 growing season had 66 days with a daily mean rooting zone temperature >0 °C in this high elevation micro-habitat (2–3 cm below ground). The degree hours >0 °C during this period summed up to 4,277 °h corresponding to 178 °d (degree days), the absolute winter minimum was –20.9 °C and the absolute summer maximum 18.1 °C. The mean temperature for the growing period was +2.6 °C. All plant parts, including roots, experience temperatures below 0 °C every night, even during the warmest part of the year. On clear summer days, plants may be physiologically active for several hours, and minimum night temperatures are clearly above the freezing tolerance of *Saxifraga oppositifolia* in the active state. In comparison with climate data for other extreme plant habitats in the Alps, Himalayas, in the Arctic and Antarctic, these data illustrate the life conditions at what is possibly the coldest place for angiosperm plant life on earth.

**Keywords** Mountain climatology · *Saxifraga* · Bryophytes · Mites · Collembola · Fungi · Isotopes

## Introduction

While bacteria and actinomycetes can be found at around 8,400 m, close to the summit of Mount Everest, and lichens were recorded at 7,400 m in the Himalayas and on top of Kilimanjaro (Swan 1992 and other references in Körner 2003) and in even more adverse conditions at 86° S and 1,980 m elevation in Antarctica (Wise and Gressitt 1965), higher plants need temperatures above 5 °C to grow, mature their seasonal foliage and reproduce (Körner 2003). Angiosperms have been recorded up to 6,400 m in the central Himalayan (30° N), 4,100 m in the Central Caucasus (43° N) and at several places in the Alps at >4,200 m at 46° northern latitude (compilation in Körner 2003) and at up to 81° N in the Arctic (Bay 1992) or 68° S in the Antarctic (Smith and Poncet 1987). Bryophytes hold an intermediate position, commonly found in higher locations/higher latitudes than the uppermost/highest latitude angiosperms. There are records up to 4,559 m for the Alps (Vaccari 1914) or for 84.4° S at 700 m elevation, close to the South Pole (Wise and Gressitt 1965). Animals and microbes are found wherever traces of plants or their debris occur, with mites holding the low temperature record at 85.3° S and 975 m elevation in the Antarctic (Wise and Gressitt 1965). The present article reports what are likely the highest habitats for an angiosperm and for perennial invertebrate animals in Europe, and it explores the temperature conditions in relation to reports from other sites of low temperature limits of plant life. The data illustrate the life conditions at the cold edge of higher plant life and its dependent animal and fungal decomposer community.

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High elevation records have to be viewed from a climatological, rather than an elevation perspective, simply because it is the microhabitat's climate rather than meters above sea level that drive life. This is best exemplified by the high elevation treeline, which may be found at 700 m a.s.l. near the northern latitude polar circle and reach 4,800–4,900 m a.s.l. in Tibet and Bolivia at otherwise rather similar growing season temperatures (Körner and Paulsen 2004; Hoch and Körner 2005; Miehe et al. 2007). In the case of small stature plants, climatological data from weather stations are not useful, because temperature in low stature vegetation, in combination with topography effects, deviates systematically and positively from air temperature by up to 8 K across a full season (Scherrer and Körner 2010a, b), with temperatures in sheltered locations during calm, sunny periods periodically not very different from low elevation life conditions (Körner 2003). Key to life in such cold places is the ability to utilize very short spells of warmth, with the longer-term mean temperatures or the inclusion of temperatures during dormant periods bearing little physiological and ecological meaning. Hence, assessing the cold limits of higher plant life needs in situ temperature records, at reasonable temporal resolution, such as offered here.

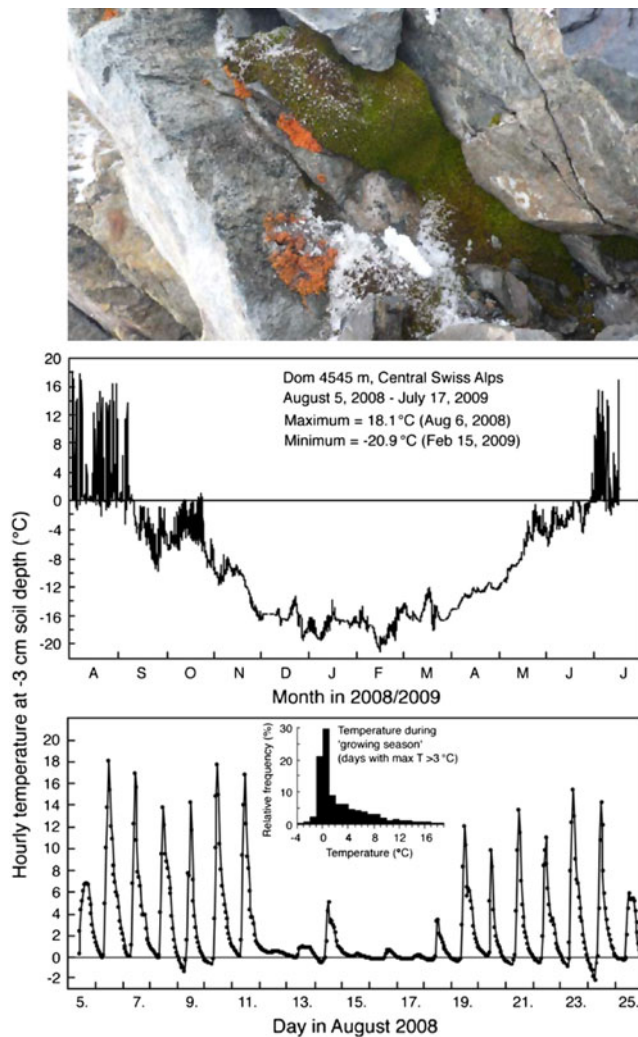
Another important distinction is physiological activity versus growth and growth versus reproduction. Respiration has been found to be ongoing in microorganisms down to  $-39^{\circ}\text{C}$  (Panikov et al. 2006), and there is no reason why this should not be the case in mitochondria of higher plants. Photosynthesis is known to continue in chloroplasts for as long as the intercellular space is not occluded with ice, which happens at around  $-5$  to  $-8^{\circ}\text{C}$  in cold-adapted plants (Larcher 1985; Körner 2003). If rated by temperature only, algae living in snow are possibly marking the cold 'edge' of eukaryotic life on earth (Kol 1935; Jones et al. 2001). To my knowledge, no higher plant has ever been found to grow (i.e., form new cells or tissue) below  $0^{\circ}\text{C}$ , but some unicellular snow algae have been shown to exhibit optimal growth (as rated by increase in cell number) at temperatures as low as  $+1.5^{\circ}\text{C}$  (Leya 2004; cf. Körner 2008), and polar marine algae thrive at year round temperatures between 1 and  $4^{\circ}\text{C}$ , supporting a rich animal food web. In addition, collembola are known to live on snow and ice (Eisenbeis and Meyer 1999; Kopeszki 2000). Higher plants, with combinations of assimilatory and heterotrophic tissue exhibit very little growth below  $5^{\circ}\text{C}$ , although roots in some species had been found expanding very slowly even at temperatures as low as  $2^{\circ}\text{C}$  (Alvarez-Uria and Körner 2007 and references therein). Temperatures between 5 and  $7^{\circ}\text{C}$  have often been treated as zero points of life (in the sense of growth and development), and this appears to hold for any cold-adapted plant from winter crops to treeline trees and to the nival flora in high mountains,

although leaf photosynthesis is active at sub-zero temperatures and may reach 30% of full capacity at  $0^{\circ}\text{C}$  (references in Körner 2008).

Successful reproduction is far more sensitive to both actual temperatures and their duration. The mere existence of flowering plants with flowers at what seems like the cold edge of life does not tell us whether these plants are able to produce viable seeds. The whole process from break of dormancy, bud swelling, flowering, pollination (if needed), fertilization, histogenesis to seed maturation needs 5–6 weeks with above freezing temperatures at the minimum for most high elevation taxa (Wagner and Tengg 1993; Wagner et al. 2010). Thus, quite often, plants at very high elevation may emerge from seeds introduced from lower elevation sources. However, the fact that these plants grow where they are, indicates that germination and seedling establishment was successful. Successful establishment may have been confined to one exceptional season within several decades of unsuitable seasons, with the remainder of life being confined to vegetative spreading (clonal growth). Such episodes are near to impossible to capture in a measurement campaign, and they may depend more on snow cover peculiarities than on temperature anomalies captured by weather stations. Successful seed maturation has not yet been reported from any continental-scale high elevation limit of plant life.

This study emerged from trying to verify an elevation record for higher plant life near the summit of the Dom, the highest mountain within the Swiss border (4,545 m a.s.l.), in sight of the Matterhorn (4,478 m a.s.l.). Anchisi (1985) mentions a record of *Saxifraga biflora* observed and reported by the mountain guides Gregoire and Pierre Nicolier in the late 1970s for an elevation of 4,450 m a.s.l. Pierre Nicolier still lives in Sion (Valaise, Switzerland) and remembers his climb, but also that he could not see the plants again on the occasion of two later climbs. The location of this finding was almost 200 m higher than the record until then for several species on Finsterhorn at 4,270 m elevation reported by Werner (1988; several *Saxifraga* species, species of *Androsace*, *Gentiana*, *Achillea* and *Ranunculus*, reference to early discoveries by Lohmeier 1872 and Calberla 1873).

When I climbed the Dom in 2008 with Juerg Anderegg (Interlaken), fierce storm and dense fog prevented us from descending from the summit to the plant location described to us by Pierre Nicolier. So we left two data loggers (one not yet recovered) at two positions (at 4,543 m a.s.l.) within 3 m distance from the summit, collected samples from a surprisingly lush moss flora in the E-face of the summit (Fig. 1) and descended the normal route to the Dom cabin at 2,960 m a.s.l. During the following summer, 2009, Juerg Anderegg climbed the Dom via Täschnhorn using the south route. Just 40 m in elevation below the summit, at 4,505 m a.s.l., 55 m above the supposed previous plant record, he found cushions



**Fig. 1** Bryophytes (see Table 1) on the E-face of the Dom summit at 4,543 m elevation and the annual course of hourly temperature readings in 2–3 cm soil depth. Below: diurnal courses between 5 and 25 August 2008, including two good and one bad (12–18 August) weather periods

of *Saxifraga oppositifolia* in full bloom (Fig. 2). He took two samples, one from each of the two biggest cushions, less than 5% of the plants, with attached debris, and he collected one of the two summit data loggers. The second logger could not be accessed because the weather turned bad again. An attempt to collect it in 2010 also failed. To place these summit records of plants and temperatures in context, I also present records from the sub-nival belt at 3,060 m, just above the Dom cabin, and readings taken with the same type of device and in the same way at the long-term observatory at Jungfrauoch at 3,460 m, and data from the arctic desert collected in Svalbard (78° N). Hence, together with data from the literature, the analysis aims at narrowing the range of most extreme low temperatures at which higher plants can live.



**Fig. 2** *Saxifraga oppositifolia* on Dom de Mischabel (Switzerland) at 4,505–4,507 m elevation, 12 August 2009

## Sites and temperature studies

### The Dom massif

The Dom summit (4,545 m, 46°5'40" N; 7°51'24" E"; Central Swiss Alps, Fig. 2a) belongs to the Mischabel group and is located at the main divide of the Alps ca 21 km NE from the Matterhorn (4,470 m) in Canton Valais. Due to regular clouds, the summit is commonly accessed in a 6-h climb via its NE snow flank from the Dom cabin via Festijoch (3,700 m a.s.l.) starting at 3 a.m., and reaching the summit by 9 a.m., just before clouds frequently close sight. Along this route, five temperature loggers were placed of which three could be recovered so far: two at 3,060 m a.s.l. and one from the summit at 4,543 m a.s.l.

The low elevation reference site in the sub-nival belt (3,060 m) was at the edge of a glacier moraine above the Dom cabin amongst open scree and rock flora, counting approximately 50 species of angiosperms in the surroundings of the two logger positions. The logging period was from 4 August 2008 to 22 August 2010. The loggers were buried 2–3 cm below ground under moss or grass, one near a *Saxifraga oppositifolia* cushion, in a rock niche facing SSW, the other one at 2 m distance from the first, at the edge of a vertical rock, open to the west, with 20 angiosperm species counted within 1 m from the logger on the level ground around.

The logger at mid-elevation on Festigrat, 3,700 m, could not yet be recovered, but this position is worth mentioning for the uppermost location of an angiosperm on this route to the summit: A very big (isolated) cushion of *Saxifraga*

*oppositifolia* forming a sort of curtain, hanging 15–20 cm from a small rock under a larger protruding rock, facing WSW, receiving lots of meltwater.

By its peculiar shape, the Dom offers snow free locations with loose substrate at an elevation permanently covered by bare rock or ice and snow in most other, even higher summits such as those of Mont Blanc (France). However, the south flanks of the Monte Rosa Massif should offer similar habitats at similar or even slightly higher elevation (Italian side of the Dufourspitze summit 4,634 m a.s.l. or Punta Gnifetti 4,559 m a.s.l.). Loggers were placed on 5 August 2008, and the one from a narrow E-facing rock crevice, with a rich bryophyte and lichen flora (Fig. 1), ca 2 m beneath the summit at 4,543 m, was collected on 5 August 2009. The other logger on a small, south facing terrace among rocks, ca 3 m south of the summit (ca 4,543 m a.s.l.) is still in place.

#### Comparative locations at Jungfrauoch and in Svalbard

Rocks behind the Jungfrauoch research station (3,469 m a.s.l., 46° N) offer very similar plant habitats in crevices as found near the Dom cabin. Two loggers were installed under light grass (*Poa laxa*), herb (*Draba* sp.) and moss cover in summer 2010 (8 July to 22 September), but given their readings were identical, only readings of one are reported here. An additional logger was installed in complete shade, 2 m above ground, behind the station as a reference (meteorological air temperature standard).

The archipelago of Svalbard extends to 80° N toward the North pole, and hosts polar deserts at its outskirts, where only very few species can survive, among them *Saxifraga oppositifolia*, *Papaver dahlianum* and *Luzula confusa*. I will show temperature data from a location at 450 m a.s.l. near Longyearbyen, where ca five species of higher plants have been found (78°14' N, 15°14' E; Gruve three fjellet at Plateau-Fjället). Two data loggers of the same type as used on the Dom had been placed in the very same way, 2–3 cm under the sparse vegetation of this arctic semi-desert (readings hardly differed, so only the mean for both loggers is shown here).

#### Temperature measurements

All temperatures were recorded with single channel temperature data loggers (Tidbit; Onset Computer Corporation, Cape Cod, MA, USA; –30 to +70 °C, 0.2 K resolution, 3 cm diameter, 1.5 cm thickness) as they had been used for previous surveys (Körner et al. in Nagy et al. 2003; Körner and Paulsen 2004). These completely sealed instruments were programmed to record temperatures at hourly intervals and were calibrated in ice water for zero degree before and after in situ exposure, but there were no deviations from zero >0.2 K. Unfortunately, the brand new logger on the Dom

summit stopped recording on 17 July 2009, so when it was collected on 12 August 2009, 18 days were missing to complete the full year, beginning on 5 August 2008. Given this data gap right in the middle of the season (statistically much better than if either the early or late part were missing), it was assumed that the frequency distribution of temperatures during the gap is similar to that before and after the gap. Hence, the length of the growing season and thermal sums of the season were scaled to the period including the 18 day data gap.

The definition of growing season is rather delicate under such extreme life conditions. Conventional thresholds for the onset and end of the season (e.g., last and first frost or absence of snow) would not work here. We adopted four definitions and offer data for all four. The first two definitions are using the first and last day with either a maximum temperature of at least 3 °C or a daily mean of >0 °C irrespective of the weather between these dates. The third definition represents the number of days per year with a maximum temperature of at least 3 °C, and the fourth definition stands for the number of days with a daily mean temperature of >0 °C. For the latter two definitions, degree hours and degree days were calculated (the sum of temperatures above the threshold, with °d = °h/24). As the results will show, these definitions have only moderate effects on the season length, but substantial effects on degree hours.

#### Biological samples

The *Saxifraga oppositifolia* voucher from the Dom summit is deposited at the Herbarium of the Institute of Botany of the University of Basel. Bryophytes had been identified and vouchers deposited at the moss herbarium of the Institute of Systematic Botany at the University of Zürich.

The debris and attached substrate under *Saxifraga oppositifolia* collected at 4,505 m elevation was examined for animals, seeds and traces of fungal presence under a dissecting and a light microscope. The organic debris contained a surprisingly high density of collembola and an incomplete part of one mite, which had been sent for identification to the Senckenberg-Museum (Görlitz, Germany), and voucher samples of collembola in 70% ethanol are deposited there. Ethanol-stored specimen were dried and used for scanning electron microscopy. Fungal traces and seeds were identified at the agricultural research center Agroscope (Reckenholz, Switzerland), pictures taken with a light microscope.

Mosses on Dom form compact, up to 4 cm thick cushions with remains of previous growing seasons well layered. This made it tempting to explore the <sup>14</sup>C age of the lowermost layer using <sup>14</sup>C signals from the 1956 atmospheric nuclear explosions. This analysis was done at the Laboratory for Ion Beam Physics, Swiss Federal Institute of Technology,

Zürich using accelerated mass spectrometry. The stable carbon isotope ratio ( $^{13}\text{C}/^{12}\text{C}$ ) of plant tissue indicates  $\text{CO}_2$  uptake efficiency and it had been shown, that the  $\delta^{13}\text{C}$  signal clearly increases (i.e., becomes less negative) with elevation and, thus, atmospheric pressure, with the slope of change steeper in the genus of *Saxifraga* than in other genera (Zhu et al. 2009). Hence, this highest sample of the European continent was examined for this signal by mass spectrometry following the procedure as described by Zhu et al. (2009; two mixed samples of green shoot material that gave similar numbers).

## Results

### Organisms

Life at this extremely high habitat turned out to be quite rich (Table 1). The mosses and lichens identified (in lichens only the two most obvious), all belong to relatively wide spread taxa. The small fraction of fresh moss cushions of *Tortula ruralis* (the biggest species; Fig. 1) were 20–30 mm thick, shrunk to 10–15 mm when air-dried, with annual increments of 0.5–1.5 mm in dry state (presumably 1–3 mm in fresh conditions), as judged by the size of the current season green top. The active layer consisted of 5–15 scale-leaves per shoot. The oldest attached dead material at the bottom of the cushion was ca 13 years old, based on  $^{14}\text{C}$ -dating (mixed sample from ca 20 moss shoots).

The individuals of *Saxifraga oppositifolia* (Fig. 2) found are the highest living angiosperm plants of Europe known so

**Table 1** List of organisms recorded at the summit of the Dom (4,505–4,543 m) on 12 August 2009

Group	Species
Angiosperms	<i>Saxifraga oppositifolia</i> L.
Bryophytes	<i>Tortula ruralis</i> (Hedw.) P. Gaertn., B. Mey & Scherb. S.L. (Syn. <i>T. norvegica</i> ) <i>Bryum bicolor</i> Dicks s.l. (Syn. <i>B. dichotomum</i> Hedw.) unidentified species, cf. <i>B. argenteum</i>
Lichens	<i>Xanthoria elegans</i> (Link.) Th. fr. <i>Lepraria aff. caesioalba</i> (B. de Lesd.) Laudon Other unidentified species
Fungi	Ascomycota, 2 species incl. one pathogenic ( <i>Sphaerotheca</i> ) Glomeromycota, 5 species incl. <i>Glomus</i> , <i>Diversispora</i> , <i>Archaeaspora</i> and <i>Paraglomus</i>
Arthropods	Collembola: <i>Thalassaphorura zschokkei</i> Handschin Mites: Acariformes, Sarcoptida (including former Oribatida species)

far, and the climatic conditions described below place these plants at the most extreme life conditions observed on earth, where higher plants do occur. The exact location is an area of about 12 m length on the south ridge, a few meters east of the Swiss GPS coordinates 632'475/104'747, ca 50–100 m of climbing distance to the summit, 2 m east from an outstanding rock column with a permanent steel loop for climbers, right on the only feasible climbing route. The slope with plants is SE- to E-exposed (sheltered by rocks in the west). There are several individuals all growing on shallow pans of loose sand between the rocks. As one loosens the sand, a dense felt of roots appears, attached to the rock surface, similar to what can be seen at the periphery of pot-bound plants.

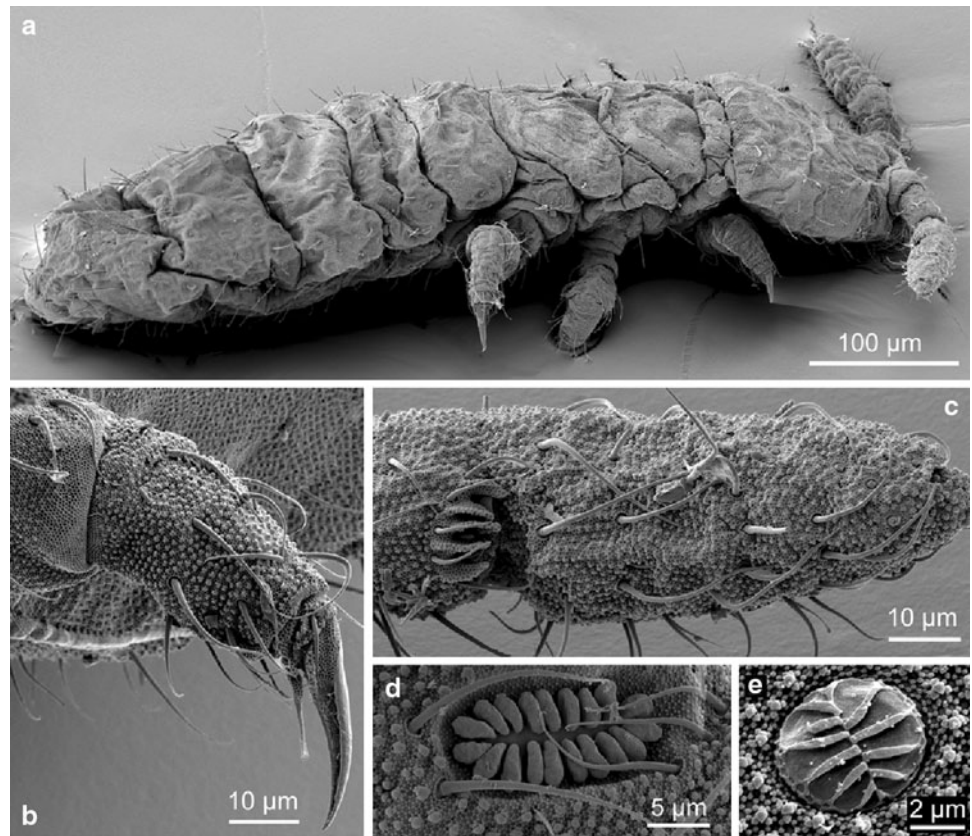
The  $\delta^{13}\text{C}$  value for *Saxifraga* foliage came at a surprise:  $-29.6 \pm 0.1\%$ , an exceptionally negative value for high elevation angiosperms, similar to means for leaves of lowest elevation plants with good water supply. Hence, the signal does not show an upslope continuation of the common elevational increase in  $\text{CO}_2$ -use-efficiency (as suggested by less negative  $\delta^{13}\text{C}$ ), despite the ca 43% reduction in atmospheric pressure and partial pressure of  $\text{CO}_2$  at this elevation. The *Tortula ruralis* moss revealed a  $\delta^{13}\text{C}$  of  $-25.66 \pm 0.2\%$  (two mixed samples) more similar to common high elevation  $\delta^{13}\text{C}$  in angiosperms.

The plant shown in Fig. 2 had dead last year flowers, flower buds and opening current year flowers. The substrate underneath contained seeds. Compared to a reference seed collection at the Institute of Botany, Basel, these seeds were smaller and their base was clearly shrunken (narrowed), suggesting pre-mature shedding, although the brown testa had the typical surface structure of *S. oppositifolia* seed (Fig. 4).

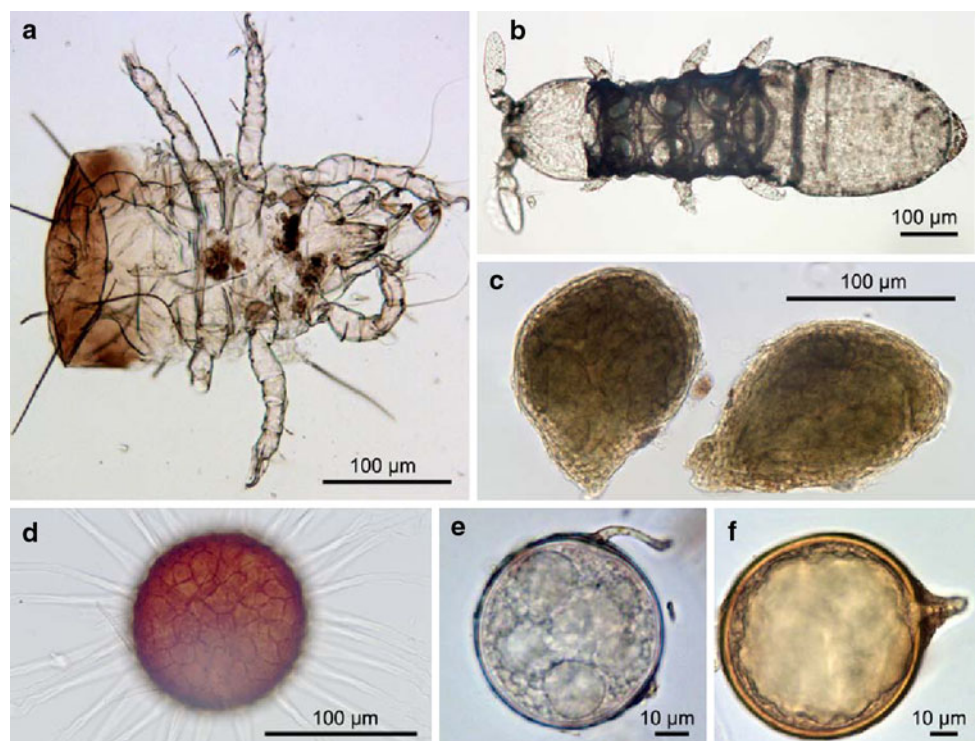
The collembola species living in the *Saxifraga* debris was identified as *Thalassaphorura zschokkei* Handschin, a rare species, known from high elevations only (Figs. 3, 4; Kopeszki 2000). Its taxonomic nature came as a remarkable finding to experts, and this species can now be attributed to be one of the highest living animal species in a permanent habitat in Europe. The other animal found is a mite, belonging to the *Oribatida* group, with only one individual in the debris examined, hence is occurring at much lower density than collembola (Fig. 4). The substrate of the ca  $5 \times 5$  cm cushion sample contained at least 30 collembola individuals (and only one mite), so the total collembola population on Dom will be several hundred individuals at least, indicating prosperous reproduction.

Fungi associated with *Saxifraga oppositifolia* belong to at least two groups, the dark septate hyphae type (Ascomycota) and arbuscular mycorrhiza (Glomeromycota) as evidenced by spores (Fig. 4). There were plenty of spores or similar structures, some of unknown nature. On all roots recovered,

**Fig. 3** SEM photograph of ethanol preserved springtails (collembola) of the species *Thalassaphorura zschokkei* (photo by D. Mathys, Zentrum für Mikroskopie, ZMB, University of Basel), **a** habitus of *T. zschokkei*, see also Fig. 4b, **b** tibiotarsus and claw, **c** sensoric postantennal organ with 19 vesicles, **d** antennal segment III and IV with antennal III organ, **e** pseudocellus (an epicuticular structure for defense), *note*: cuticle with typical hexagonal arrangement of triangular granules



**Fig. 4** Microscopic organisms found in loose substrate under *Saxifraga oppositifolia*: **a** an Oribatida mite, **b** collembola as in Fig. 3, **c** seeds of *S. oppositifolia*, **d** *Cleistothecium* (ascomycota), **e** and **f** spores of arbuscular mycorrhiza (Glomeromycota; photo by F. Oehl, Reckenholz, Switzerland)



**Table 2** Soil temperature records (2–3 cm depth) from the Dom summit 4,543 m and the nival belt at 3,060 m at the base of the Dom, Jungfrauoch 3,460 m (soil and air), the Himalayan 5,960 m and Svalbard 450 m for the growing season (various definitions)

	Dom top soil 4,543 m 46° N	Dom low soil 3,060 m 46° N	Jungfrauoch soil 3,460 m 46° N	Jungfrauoch 2 m air 3,460 m 46° N	Himalaya soil 5,960 m 32° N	Svalbard* soil 450 m 78° N
Absolute minimum (°C)	−20	−5.3	−	−	−20.0	−13.0
Absolute maximum (°C)	18.1	25.1	25.8	12.4	11.8	12.0
Seasonal mean (°C)	2.6	6.7	5.3	0.6	4.0	4.8
Mean of warmest month (°C)	2.8	9.5	7.2	2.3	−	4.7
Duration of growing season						
(a) first/last day $T_{\max} \geq 3$ °C	72	139	80	79	82	47
(b) first/last day $T_{\text{mean}} > 0$ °C	73	139	80	79	82	58
(c) days $T_{\max} \geq 3$ °C	62	122	60	43	80	46
(d) days $T_{\text{mean}} > 0$ °C	66	122	79	37	81	51
In (c) number of h $T_{\max} \geq 3$ °C	585	2,200	969	546	1,085	893
In (d) number of h $T_{\text{mean}} > 0$ °C	1,053	2,652	1,774	926	1,684	1,189
In (c) degree days (°d)	103	620	261	60	144	99
In (d) degree days (°d)	178	870	387	136	290	210

The Himalayan data were provided by J. Doležal

\* Svalbard experiences 24 h daylight in summer

there was clear indication of mycorrhization. There were also pollen grains (including conifer pollen).

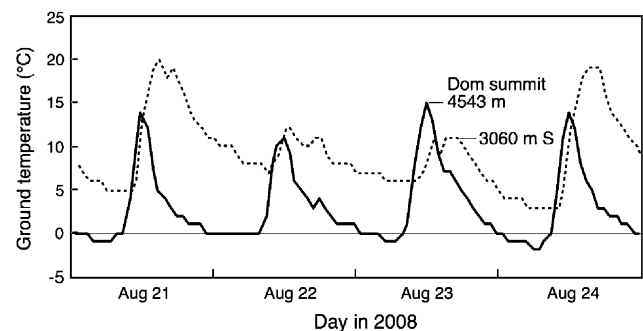
### Microclimate

The temperature conditions on the Dom summit, as represented by the signals of the single data logger that could be recovered, should be similar to what *Saxifraga* experiences at only 35–40 m elevation below (Fig. 1). Both, *Saxifraga* and the bryophyte community described above may profit from the relatively long snow free conditions on this steep escarpment and from the more frequent sunshine hours on east-exposed sites during clear morning hours (the summit is frequently in clouds from late morning onwards).

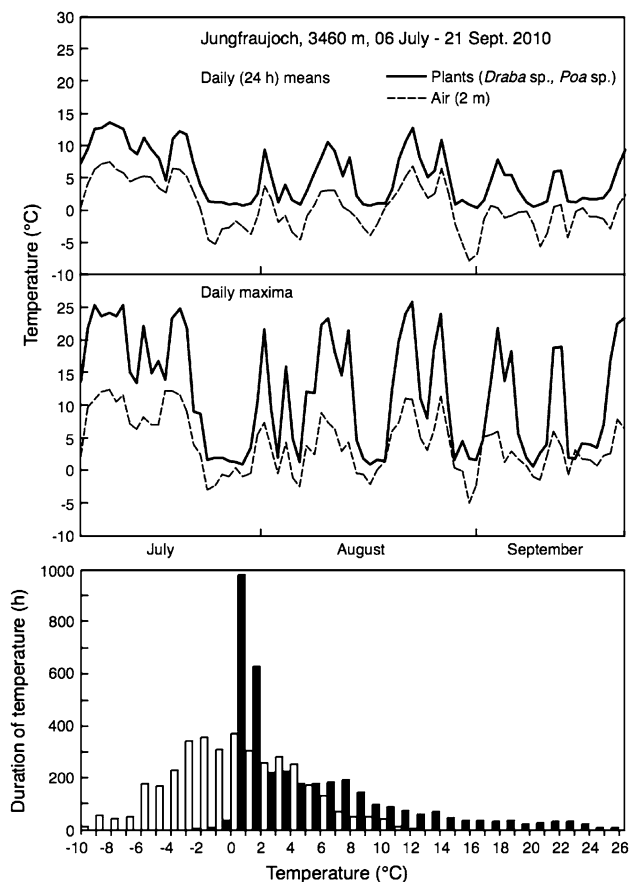
A detailed analysis of the temperature records for the growing period revealed that life at this elevation incurs daily exposure to freezing temperatures of all plant organs from flowers, leaves, shoots to roots, including the microfauna. Of the 62–73 days growing season (depending on definition, Table 2), there was no frost-free day at 2–3 cm substrate depth. Because of radiative cooling at night, foliage and inflorescence temperatures will have been lower than what is suggested by the data of the buried logger. Over the 66 day period of days with at least periodically unfrozen soil, the mean temperature was 2.6 °C. Degree days above 0, 5 and 7 °C accumulated to 178, 60 and 35 °d over that same period. While season length is relatively similar for the four different definitions, the total number of hours with temperatures above 0 °C is almost twice as high as that above 3 °C at this 4,543 m location, illustrating the dominance of ground temperatures between 0 and 3 °C as seen in the histogram inserted in Fig. 1. Ground warming at 2–3 cm

depth was quite remarkable, reaching a maximum of 18.1 °C (6 August 2008), again, with likely higher temperatures occurring amidst the cushions of mosses and of *Saxifraga* during periods of direct insolation. The lowest ever recorded temperature during the year was the −20.9 °C winter minimum (15 February 2009), not as cold as one might expect at such high elevation, most likely due to snow cover (Table 2). The transition between the dormant and growing period was very abrupt due to the disappearance of snow as indicated by the strong diurnal oscillation of temperatures when snow is absent.

At 3,060 m, i.e., at ca 1.5 km lower elevation in the sub-nival belt, the climate experienced by plants is clearly much warmer (Table 2, Fig. 5). However, given the rather different snow cover and microhabitats, there is no point by point or day by day correlation, not even during the growing



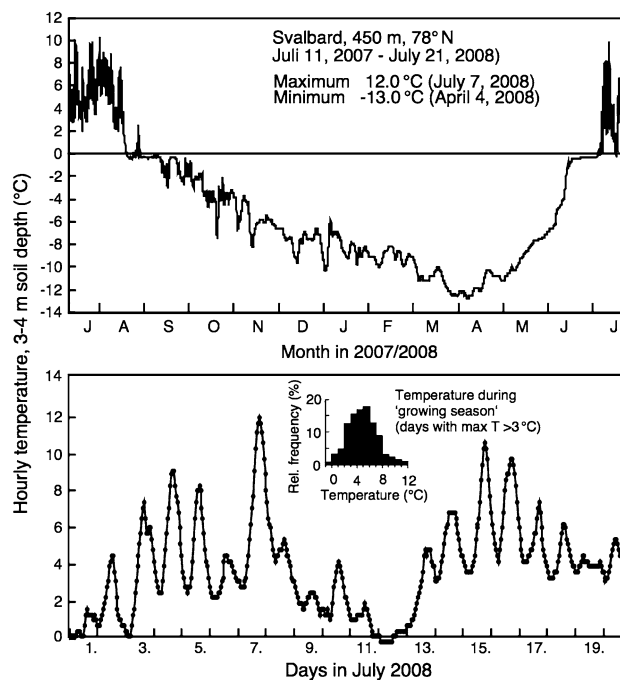
**Fig. 5** Diurnal courses of plant temperatures at 2–3 cm substrate depth under vegetation at 3,060 m in the sub-nival belt of the Mischabel (Dom) massif during a period of good weather in August 2008, dashed line, and the concurrent temperatures at the Dom summit (4,543 m)



**Fig. 6** Air (2 m) and plant temperature (2–3 cm under sparse plant cover, S-exposed) at Jungfrauoch (3,460 m) during the 2010 growing season. Note the higher plant temperatures compared to air temperature

season (data not shown). Periodically, even higher temperatures are observed on the Dom summit (Fig. 5), illustrating the effects of clouds and exposure. A remarkable difference is seen in winter: presumably due to the heavy snowpack, plants at this lower location hardly ever freeze, with root zone temperatures for most of the winter around 0 °C. Summertime maxima are far more pronounced at this lower elevation and reach 25.0 °C.

Seasonal and diurnal temperature courses at the 3,460 m a.s.l. Jungfrauoch (Fig. 6) and in Svalbard (Fig. 7) are taking a position between the lower and uppermost logging site at the Dom. The data from Jungfrauoch illustrate the large contrasts between air temperature (not available for any other location) and plant temperature (Fig. 6). Daily mean temperatures 2–3 cm below plants exceed those of air temperature on average by 5 K, and maximum temperatures (warmest hourly reading per day) are 13 K warmer in the plants' rooting zone than in air, hence, confirming that air temperature has little predictive value for plant temperature at such high elevations. For air temperature, this also finds expression in the lowest degree days of all data sets shown in



**Fig. 7** Soil (plant) temperature, 2–3 cm below ground in an arctic semi-desert in Svalbard (450 m), with *Saxifraga oppositifolia*, *Luzula confusa* and *Papaver dahlianum* (note, there is 24 h daylight)

Table 2. The air at 3,460 m is substantially cooler (136 °d > 0 °C) than the 2–3 cm rooting zone temperature on the Dom summit (178 °d) at 1 km higher elevation. The air temperatures measured at the same time at the Jungfrauoch meteorological station at 3,580 m correlated very closely with the air temperature measured here ( $T_{3460} = 1.01 + 0.98T_{3580}$ ,  $r^2 = 0.93$ ), with the zero displacement largely reflecting the 120 m difference in elevation (ca 1 K). Using the long-term meteorological records for June to September temperature at Jungfrauoch, the summer temperatures during the 2008/2009 measurement period are matching the mean for the last ten years (2000–2010), and are slightly (<0.5 K) warmer than the mean of the previous two decades (1979–1999).

The site in the polar desert in Svalbard is clearly warmer than the Dom summit with a mean growing season (only 46–51 days, depending on definition) temperature of 4.7 °C, largely due to the 24-h day length and thus, greatly diminished radiative cooling during the polar 'night', although with a lower solar angle than during the polar 'day', contributing to diurnal variation in temperature.

## Discussion

It does not come at a surprise that *Saxifraga oppositifolia* holds the high elevation and presumably low temperature record of Europe. It also is one of the two polar high



elevation record species in Svalbard (the other is *Papaver dahlianum*, at 915–940 m at 78° N; Sunding 1962). The Arctic high latitude record of angiosperm life including *S. oppositifolia* is at Greenland, at 83°38' N under maritime influence (Bay 1992). But at this location, only ca 7° south of the North Pole, 50 angiosperm species have been recorded according to Bay.

*Saxifraga oppositifolia* had been examined intensively for its low temperature resistance, and it can be rated as 100% freezing resistant. During winter dormancy this species had been found to survive dipping in liquid nitrogen (Larcher et al. 2010), and low temperature episodes during the growing season are much warmer than what this species can tolerate. On the one hand, its small size, slow clonal growth but lush flowering, soon after snowmelt (from preformed buds, early flowering phenotype, Molau 1993; Gugerli 1998) appears well suited for life under such conditions. Yet, successful reproduction is highly unlikely. It was shown that seeds may take up to 11 weeks to mature in this species (Wagner and Teng 1993), much longer than in other high elevation species (Ladinig and Wagner 2005) suggesting that successful seed production must be rare (if possible at all) at such elevations, and, thus, recruitment is likely to depend on seed sources from lower elevation. Although *Saxifraga oppositifolia* had the shortest (6–10 days) pre-floration period (from snowmelt to flowering) of several extreme high elevation taxa, it exhibited the longest histogenesis period (32 d), and total seed development period (46 d, excluding the period until zygote formation) of several other *Saxifraga* species in the sub-nival belt (Wagner et al. 2010). However, we do not know if the individuals found at Dom belong to 'faster' ecotypes as discussed by Wagner et al. (2010). Though traces of seeds were found in the debris, the very late flowering in the study year (mid August) and the distorted shape of the older seeds found under the cushion make it very unlikely that seeds are able to mature at this location, except perhaps under unusual weather conditions. The fact that no other plants are found than those within that ca 12 m zone on the ridge, suggests that local reproductive propagation is rather limited. The extremely tiny seeds may facilitate spreading by wind and cause this to become a very successful pioneer species, obligatorily contributing to summit floras and to high arctic deserts. According to Wagner et al. (2010), *Ranunculus glacialis* or *Saxifraga biflora* would be in a far better position to produce mature seeds at such an extreme location.

In contrast, the well developed bryophytes right at the Dom summit do not belong to a specialist category and reflect the general tolerance of mosses to very short growing seasons and to a wide spectrum of harsh habitat conditions. Their occurrence rather seems to reflect random effects. Moss occurrence also does not depend on soil temperature. In fact mosses intercept solar heat so effectively, that the soil

under mosses stays colder than without (Gornall et al. 2007). A similarly high elevation record for moss (*Grimmia incurva*) occurrence was reported by Vaccari (1914) for Punta Gnifetti (4,559 m, Monte Rosa). The species most vigorously growing on the Dom summit, *Tortula ruralis*, was also recorded by Vaccari (1914) at a maximum elevation of 3,559 m on Monte Emilius, also in the western Alps. Record moss elevations for the Alps were also reported for the (lower) eastern part on the summit of Weisskugel 3,734 m (*Rhacomitrium lanuginosum*, *Grimmia doniana*) and the (higher) western part on Balmenhorn 4,231 m (*G. doniana*; Pitschmann and Reissigl 1954; Maier and Geissler 1997). According to the <sup>14</sup>C dating, the oldest part of individual 25 mm long shoots may not be older than 13 years. However, in the light of its size and spreading (Fig. 1) and the slow growth, the hump-shaped cushion as such must be much older. If one assumes a similar rate of vertical and horizontal expansion of the clone, a 75 mm cushion radius would correspond to half a century. During this period, the climate clearly became warmer in the Swiss Alps than it was before (Beniston 2004).

In the study year (a rather 'normal' year, see Jungfraujoch, below), the temperatures recorded at the Dom summit were harsher during the growing season than those measured on Mt. Brunnenkogel (3,440 m, Ötztal Alps, Austria, similar latitude) by Larcher and Wagner (2009), and similar to those measured in the Ladakh Himalayan (5,960–6,030 m) by Klimeš and Doležal (2010), in both cases at the regional upper limit of plant life. The Himalayan data have been collected deeper (–5 cm) in soil above permafrost and, thus, should be cooler than the corresponding 2–3 cm depth temperatures recorded in the Alps and in Svalbard. On Brunnenkogel minimum plant canopy temperature was mostly above zero (extreme –4.5) during midsummer, maxima reached 28 °C (extreme 31.4 °C) with 43% of all hours between 0 and 5 °C and a growing season (in this case snow free period) mean of 3.6 °C. The winter minimum (under snow) was –15 °C.

For the Himalayan site, the growing season, defined in exactly the same way as on Dom (Table 2), lasted longer (80–82 days) and the hours above the same thresholds as well as the degree days indicate a substantially warmer microclimate, with a seasonal mean soil temperature at 5 cm depth of 4.0 °C (and a minimum of –18.1 °C in winter). The authors noted that soil temperature dropped below freezing every night during summer, presumably also related to the permafrost close to the surface (mentioned by the authors). Soil temperatures exceeded 2–4 °C every day during the growing season, but only for a few hours. Top soil and canopy temperatures must have been considerably warmer than this –5 cm record.

Mahringer (1964) reported unsheltered soil temperature at 2 cm depth from Sonnblick (3,100 m Austrian Alps) and

found August means of 5.1 °C with maxima between 26 and 28 °C (11–12 °C for air) and a minimum for midsummer of only –0.7 °C, because bad weather is associated with snow cover at this elevation. During the day, canopy temperature at the Dom summit will be warmer than the one reported here for substrate, due to trapping of solar heat among foliage (Körner and DeMoraes 1979; Larcher and Wagner 2009) and perhaps, enhanced by some re-radiation by the surrounding rocks (Fig. 2).

Substantially warmer temperatures are reported for habitats of the two only angiosperms in Antarctica. During late summer, air temperature varied between 0 and 10 °C and –2 cm soil temperature went up to 30 °C with a mean of around 10–15 °C for most of the days. Soils remained unfrozen during this period (data for *Colobanthus quitensis* and *Deschampsia antarctica* on Signy island, 60° S, March 1989, by Smith 1994). Hence, the poor representation of angiosperms in this region rather seems to be related to the lack of hardy taxa than to the climate during the growing season. At cooler growing season temperatures, at the most northern edge of Greenland, 50 species were found (Bay 1992), and the far colder arctic desert of northern Svalbard is also much richer in species (>20, personal observation). Temperatures measured in *Bryum argenteum* moss cushions in Antarctica (78° S) during peak season (17–31 January 2003; Burkhard Büdel, pers. com.) reached a maximum of 12.5 °C and averaged around 4–6 °C during the polar day with freezing in almost every polar ‘night’ in midsummer. Air temperatures were 5–10 K lower than moss temperature.

It is well known that ground and ground surface temperature, as well as plant canopy temperature at high elevation are largely controlled by exposure (slope inclination and direction). Rock temperatures may hardly ever exceed 0 °C on a N-facing slope at 3,700 m in the Alps, but rise above 30 °C (recorded extreme +43 °C) every day with sunshine on S-slopes, even at extremely high elevations of >3,700 m (Mathys 1974; Wegmann 1998).

Heat storage in dark rock around crevices or niches with plants may rise soil temperatures also during at least the early part of the night and may co-explain the root crowding at the rock-sand interface observed under *Saxifraga* on the Dom summit. Hence, the length of the growing season is a matter of exposure rather than elevation and can only be defined at a plant level as had been noted many times (an early summary by Winkler 1953; Körner 2003; Larcher and Wagner 2009). In his synthesis, Winkler assumes air temperature minima >0 °C to be a good proxy for days with growth conditions on sun exposed sites. Using this threshold, the growth period lasted 40 days on Jungfraujoch according to Winkler’s assessment, and 37 days, 60 years later in the current assessment that started only on July 8, hence was missing at least 2–3 weeks. Both numbers clearly underestimate the length of the actual growing season

(Table 2), given that soils may warm by 5–13 K over air temperature even under frosty conditions as shown here (Fig. 6), with the short plant canopy presumably even warmer. Periodic (night-time) freezing is no problem for plants like *Saxifraga oppositifolia* and they may use any single ‘warm’ hour during the day for growth, similar to winter crops (Körner 2008). As soon as leaves thaw (which means resorption of water from intercellular spaces following from intercellular ice produced during freezing) photosynthesis and all other life processes are resuming (Larcher and Wagner 1976; Körner 2003).

The  $\delta^{13}\text{C}$  value for *Saxifraga oppositifolia* from the Dom summit is placing this sample outside the multi-species regression against elevation for other *Saxifraga* species, including *S. oppositifolia*. The mean value found at the Dom is rather matching the signals from lowest elevation specimens (Körner et al. 1991; Zhu et al. 2009). Hence, the increasingly thin atmosphere known to cause  $\delta^{13}\text{C}$  signals to become less negative by 1–1.5‰ per km has not had any impact on the CO<sub>2</sub> uptake efficiency of this specimen, and there was also no water shortage during biomass formation, as far as one can tell from such isotope data.

In conclusion, life on the Dom summit at >4,500 m includes at least 16 different eukaryotic taxa, less than half of which autotrophic: 3 moss species, >3 lichen species, 1 angiosperm, 2 arthropod species, and 7 fungal species, 6 symbiotic, 1 parasitic. A more in-depth study could bring this list easily to much higher numbers (including further fungi and lichens as well as algae) in what might be one of the coldest, if not the coldest terrestrial microecosystem on earth with angiosperms. Including prokaryotes (bacteria) might double species diversity to twice the eukaryotic one under such sheltering high elevation plant cover (Schinner 1982).

A 60–70-day growing season (defined by days with at least 1 h >3 °C or a daily mean >0 °C in the uppermost rooting zone), and a seasonal mean top soil (root zone) temperature around 2.6 °C at roughly 180 °d > 0 °C over the entire season seem like the minimum for persistent (clonal) angiosperm life (disregarding sexual reproduction). Klimeš and Doležal (2010) tested whether plants can be transplanted beyond their current upper elevational limit in the Himalayan, and they failed when season length dropped below 6 weeks in this otherwise slightly warmer, lower latitude environment. The Dom’s *Saxifraga* occurrence may be seen as a result of a natural ‘transplant’ experiment that took advantage from one or few favorable seasons in the recent past. Once established, such clonal plants can persist even beyond the species’ reproductive range, pointing at the critical role of plant establishment. Lichens need only a few days per year to live, according to Pannewitz et al. (2003), 10–14 days of moist, above zero temperatures are sufficient at 77° S in the Antarctic. Moisture is far more critical in

lichens than temperature, given the means for the warmest month at that Antarctic location were between 2.5 and 4.5 °C, i.e. on average significantly warmer than on the Dom summit (Schroeter et al. 2010).

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