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Survival types of high mountain plants under extreme temperatures

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A B S T R A C T

Extreme temperatures are a main factor limiting plant growth in high mountain habitats. During winter, the risk of frost damage is highest at windblown and often snow-free sites. During summer, actively growing plants are particularly endangered by episodic cold spells, but also by short-term overheating. The current review gives an overview of extreme temperatures in the European Alps and observations of temperature damage on plants in their natural habitats. Furthermore, seasonal time courses of frost and heat resistance derived from laboratory tests on different plant growth forms are presented. Study species were the cushion plants *Silene acaulis*, *Minuartia sedoides*, *Saxifraga oppositifolia* and *Carex firma* collected on wind-exposed ridges; the rosette plant *Soldanella alpina* collected on snow-protected sites, and three *Sempervivum* species collected in xerothermic habitats.

The temperature resistance of leaves, stems, rhizomes and roots were tested in two annual time courses. Frost treatments were conducted in controlled freezers by rapid cooling ($10\,\mathrm{K\,h^{-1}}$, for current resistance) as well as by stepwise cooling ($1–3\,\mathrm{K\,h^{-1}}$, for hardening capacity). Heat treatments followed a standardised procedure by exposing samples to heat for 30 min in hot water baths. The damage was visually estimated using the topographic tetrazolium test.

During winter, cushion plants from exposed sites were fully hardened (LT_{50} below −70 °C). Rosette plants, which are protected by a constant snow cover, survived temperatures of down to −25 °C. During the growing period, foliage and shoot tips of the investigated species were damaged at −5 to −8 °C (LT_{50}). Stems and rhizomes were only partially damaged by temperatures of −10 to −15 °C. Heat resistance in cushion plants generally reached 56–58 °C (LT_{50}), shoots and rhizomes of *C. firma* could reach 60 °C. Succulent plants like *Sempervivum arachnoideum* and *S. tectorum* from hot and dry microsites were the most heat resistant among the tested species (62–64 °C). The investigated mountain plant species showed highly varying resistance patterns, with variation in maximum hardening capability and seasonal time courses of resistance. Plants were capable of rapid adjustments to extreme temperatures, which is crucial for survival in a high mountain climate.

Introduction

Among the various environmental factors in the mountains, the climate operates as an altitudinal selection filter and adaptation force (Larcher, 1980). Above the timberline, air temperatures and microclimate temperatures become more extreme and thus limiting. Therefore, only specialised mountain plants can survive in these high altitudes. During the main growing period, high mountain plants are particularly threatened by temperature constraints such as frosts caused by cold spells but also short-term overheating. During winter, the risk of frost damage is relatively low for prostrate plants that are permanently covered with snow at constant temperatures of between 0 and −5 °C (e.g. Aulitzky, 1961; Aulitzky et al., 1982). On windblown and often snow-free sites, however, plants must be fully frost resistant to survive temperatures of down to −30 °C and lower (e.g. Franz, 1979). In summer in the alpine zone, rosette and cushion plants in wind-protected niches bear the greatest risk of overheating, particularly if solar radiation is high and precipitation low (Buchner and Neuner, 2003; Körner, 2003; Larcher and Wagner, 1976).

Frost and heat resistance of herbaceous mountain plants at mid and higher latitudes have been the subject of a number of studies. Most data stem from the European Alps (e.g. Buchner and Neuner, 2003; Kainmüller, 1975; Larcher and Wagner, 1976, 1983; Neuner et al., 1999, 2000; Pisek et al., 1967, 1968; Taschler and Neuner, 2004; Ulmer, 1937), with some additional data from mountains of Scandinavia (Gauslaa, 1984; Junttila and Robberecht, 1993; Robberecht and Junttila, 1992), and the temperate mountains on other continents (Bannister et al., 2005; Marchand et al. 2006; Mooney and Billings,1961; Sakai and Otsuka, 1970). Most investigations concerned frost or heat resistance of leaves and

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shoots during the growing season. Less information is available about temperature resistance during winter (Junttila and Robberecht, 1993; Sakai and Otsuka, 1970), and hardly anything is known about resistance changes in the course of a year (Bannister et al., 2005; Kainmüller, 1975). Similarly rare are reports about the temperature resistance of belowground organs (Kainmüller, 1975; Sakai and Otsuka, 1970).

We investigated species of different growth forms from various habitats including cushion plants growing on rocky locations, rosette plants needing constant snow cover as well as species growing in xerothermic mountain habitats. The current resistance, the maximum resistance (by hardening) and the minimum resistance (by dehardening) of vegetative aboveground and belowground organs were determined in the course of a year. In some cases some insight could be gained from the synergism between frost resistance and heat tolerance through winter drought. The data mostly stem from investigations carried out between 1970 and 1980, which have not yet been published or at least not in full.

This publication should bridge the information gap on whole plant resistance of herbaceous high mountain plants and their seasonal resistance dynamics. This capability of adjusting to seasonally changing temperatures determines a species' perseverance in stressful habitats and shows species-specific limits, which can arise as a result of changes in climate. Current projects dealing with susceptibility to extreme temperatures of flower buds, open flowers, developing and germinating seeds, and survival of seedlings in open habitats – will give further information about reproductive fitness under extreme temperatures and thus a species' capability of maintaining population turnover and colonising new habitats.

Extreme temperatures in high mountain regions

In the Alps the absolute lowest air temperatures ever measured in standard weather stations were −36 to −37 °C (Cappel, 1977; Steinhauser, 1954; Swiss Institute for Meteorology, 1930). These temperatures are of course exceptional. Most of the absolute minimum air temperatures of the free atmosphere in winter range from −17 to −24 °C in the alpine altitudinal zones and from −23 to −30 °C in glacial regions (Table 1). During the growing season (June–August) freezing temperatures are also dependent on the altitudinal zones. In the alpine zone absolute minimum air temperatures observed are −7 °C in June and −3 to −4 °C in July and August whereas at the height of summer (July, August) frosts of about −7 °C occur in the subnival zone and −8 to −10 °C in glacial regions.

In high mountain regions, considerable temperature differences can be measured between the free atmosphere and the boundary layer climate. This is exemplified by two annual boundary layer temperature curves from microsites in an upper alpine zone (Mt Hafelekar; Fig. 1) and a subnival region (Stubai Glacier; Fig. 2). Plant temperatures were recorded at hourly intervals using small data loggers of 3 cm diameter and 1.2 cm height with a NTC-pearl sensor ("StowAway Tidbit", Onset Computer Corp. Pocasset, MA, USA). On the sites with open vegetation, loggers were placed in plant cushions so that the sensors were shaded by leaves. Temperature databases also indicated the duration of snow cover at the different sites.

In winter, prostrate plants are mostly covered with snow. Beneath a layer of snow thicker than 50 cm the temperature in winter seldom sinks below −5 °C in intermediate latitudes (Aulitzky et al., 1982; Sakai and Larcher, 1987). At sheltered microsites in the alpine zone, plants can survive temperatures between 0 and −3 °C until the end of May. Under a thin snow cover and on windy ridges plants, particularly pioneer plants, have to endure air temperatures; this means that on the western slope of Mt Hafelekar, where *Silene acaulis* and *Saxifraga oppositifolia* grow, the temperatures range from −8 to −14 °C due to strong snow-drift in winter. Also the study site on the Stubai Glacier is very much exposed to wind, which is why cushion plants (e.g. *Saxifraga bryoides*) frequently grow there. Microclimate temperatures as low as −20 to −22 °C have been measured there.

After the thawing period and during the growing season there are repeated frosts in the sparse vegetation and on the soil surface. In midsummer (July and August) about 20 frost days (between −2 and −3 °C) were recorded in the subnival ecotone and about 50 frost days (down to −5 °C) on a nival summit. Clear nights can induce particularly low temperatures in the morning due to thermal re-radiation.

High microclimate temperatures in mountain regions are brought about by intensive incoming radiation, shelter from the wind and dry superficial soil on southern and south-western inclinations. During summer, prostrate plants of the alpine zone repeatedly reach maximum noon temperatures of 30–35 °C with temperatures occasionally reaching 40 °C (Larcher and Wagner, 1976). Cushions were found to be 16–25 K warmer than air (Körner and DeMoraes, 1979). On a clear day in midsummer maximum temperatures of 35 °C were measured for *S. acaulis* and

Table 1
Monthly absolute minimum (*Tmin abs*) air temperatures at 2 m height above ground level and mean absolute minimum temperatures (*mean abs*) in high mountain regions in the Central Alps.

Months	**Patscherkofel** (1995–2006)		**Mittelberg** (1995–2006)		**Sonnblick** (1995–2006)		**Brunnenkogel** (2003–2006)
	Tmin abs	*Mean abs*	**Tmin abs**	*Mean abs*	**Tmin abs**	*Mean abs*	**Tmin abs**
January	**−21.8**	*−17.4*	**−27.0**	*−21.4*	**−29.4**	*−23.5*	**−29.1**
February	**−23.8**	*−17.2*	**−29.0**	*−22.0*	**−30.3**	*−22.7*	**−30.8**
March	**−22.5**	*−16.0*	**−26.3**	*−21.4*	**−30.0**	*−22.4*	**−28.4**
April	**−18.8**	*−12.3*	**−23.4**	*−17.3*	**−25.0**	*−18.1*	**−20.0**
May	**−8.6**	*−5.9*	**−14.7**	*−10.8*	**−14.6**	*−11.4*	**−18.6**
June	**−6.9**	*−2.9*	**−14.0**	*−6.5*	**−12.3**	*−8.1*	**−14.7**
July	**−2.8**	*−0.1*	**−7.0**	*−3.7*	**−8.0**	*−5.1*	**−9.0**
August	**−3.8**	*−0.1*	**−7.3**	*−4.0*	**−9.0**	*−5.4*	**−10.5**
September	**−6.4**	*−3.3*	**−11.4**	*−7.2*	**−13.0**	*−9.1*	**−11.9**
October	**−12.9**	*−6.4*	**−19.4**	*−10.5*	**−19.5**	*−12.4*	**−22.2**
November	**−19.4**	*−13.5*	**−23.0**	*−18.1*	**−24.9**	*−19.2*	**−23.1**
December	**−23.4**	*−17.3*	**−26.3**	*−21.0*	**−30.5**	*−22.7*	**−29.3**

Alpine vegetation zone: *Mt Patscherkofel* (2247 m a.s.l.; about 8 km south of the study areas of Mt Hafelekar 2334 m a.s.l.). Alpine-nival ecotone: *Mittelbergferner* glacier foreland (2850 m a.s.l.; about 19 km south of the study areas of Stubai Glacier, 2880 m a.s.l.). Nival zone: *Mt Sonnblick* (3106 m a.s.l.; Hohe Tauern) and *Mt Brunnenkogel* (3440 m a.s.l.; Ötztal Alps). Data were obtained from the Central Institute for Meteorology and Geodynamics (www.ZAMG.ac.at).

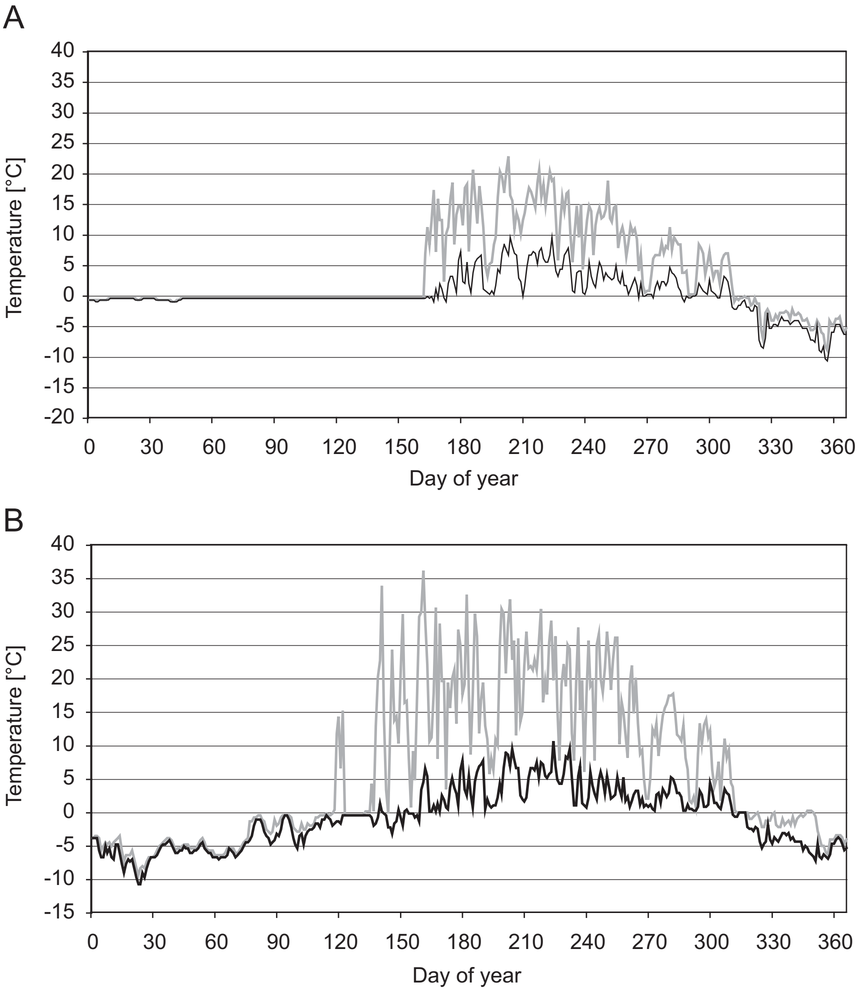

Fig. 1. Annual course of boundary layer temperatures on Mt Hafelekar in the climatically normal year of 2004: (**A**) data logger on a snow-rich, northern location (2324 m a.s.l.); (**B**) data logger on a windy western ridge (2314 m a.s.l.). *Upper line*: daily maximum; *lower line*: daily minimum.

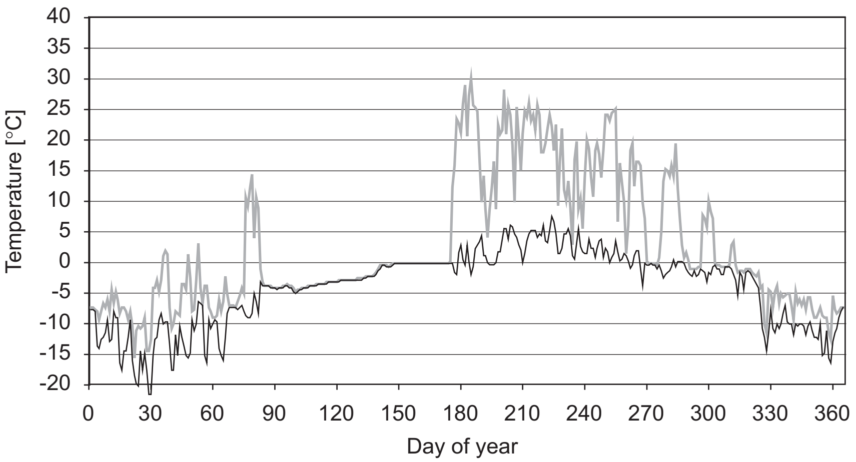

Fig. 2. Annual course of boundary layer temperatures at a subnival site in the Stubai Glacier foreland (2880 m a.s.l.) in the climatically normal year of 2004. The temperature logger was installed in a cushion of *Saxifraga bryoides. Upper line*: daily maximum, *lower line*: daily minimum.

S. oppositifolia with an infrared pyrometer (PRT-10L, BARNES, Stamford, USA) at their growing sites on Mt Hafelekar. During calm weather the cushions of *Carex firma* heated up to 46 °C; the highest plant temperature was 48 °C measured in a dry *Carex* cushion. Even higher temperatures were found on rosettes of *Sempervivum montanum* on Mt Patscherkofel (Larcher and Wagner, 1983). When solar radiation is intense and wind is absent *Sempervivum* rosettes can heat up to over 40 °C, and on midsummer days we repeatedly measured leaf temperatures of about 50 °C (Fig. 3).

The air temperatures in the nival zone are so low (maximum temperatures during midsummer of 17 °C at 2850 m a.s.l. and

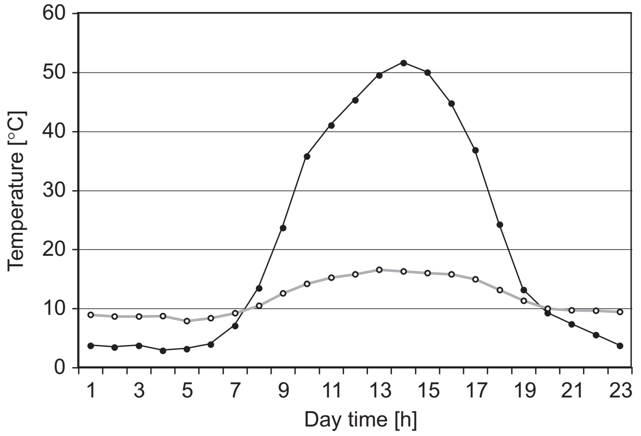

Fig. 3. Diurnal course of temperatures on a clear midsummer day (1973-08-14) on Mt Patscherkofel (2200 m a.s.l.): ○—○ air temperature at 2 m height; ●—● temperatures within rosettes of *Sempervivum montanum.*

12 °C at 3440 m a.s.l.) that high plant temperatures happen very rarely even when radiation is intense. On Mt Brunnenkogel we measured plant temperatures of 30 °C.

Damage to high mountain plants in natural habitats caused by extreme temperatures

The survival capability of plants in climatically extreme regions can be estimated by assessing climatic injuries in the field and experimental tests. Field observations after injurious events present valuable data about the limits of hardiness of various plants under natural conditions. In addition after-effects as well as the chances of recovery can be observed. However, these damage assessments are often vague as irregular climate monitoring makes it difficult to link the damage to specific temperature events. Nonetheless, every opportunity should be taken to record naturally occurring frost and heat damage in order to verify experimental data.

Frost damage in the natural habitat

High mountain plants are especially endangered by frost during the growing period. In the alpine zone, young shoots and flowers of *Rhododendron* species and of the dwarf heath shrubs (*Vaccinium* species in particular) can suffer damage from late frosts of about −4 to −7 °C until the end of May and June. Proliferating inflorescences and opened flowers of *Rhododendron ferrugineum* are already partly damaged by temperatures of −3 °C. During a frost event of −5 °C in June 1999 up to 90% of the reproductive and vegetative shoots in *Rhododendron* stands were affected (Larcher and Wagner, 2004).

In the subnival and nival zone summer frosts of −7 to −9 °C occur repeatedly as a consequence of cold waves, which are mostly accompanied by slight snowfall. This snow cover protects the prostrate vegetation from low temperatures. Frost damage usually occurs only when snow cover is missing or insufficient. During two sudden cold waves in July 2007 the temperatures in the glacial region sank to −5 to −7 °C. Shortly later, at the beginning of August the plants on Mt Brunnenkogel (3440 m a.s.l.) were visually assessed for frost damage. Vegetative shoots of rosette and cushion plants did not show any visual injury whereas reproductive shoots did. Several blossoms of *Ranunculus glacialis* froze to death, in which case the corollas were severely damaged and more than half of the anthers and carpels suffered damage. The vegetative organs were, however, free of damage. Flower buds and open blossoms of *Minuartia sedoides* were fully damaged. Also in the case of *S. bryoides*, which was in the middle of anthesis, almost all buds and flowers (styles in particular) were damaged. Blossoms of *Leucanthemopsis alpina* were partly damaged, with ray flowers more sensitive than tubular flowers. Several plants of *Cerastium uniflorum* showed blossoms with signs of frost damage but intact leaves.

During winter, frost damage basically only occurs on occasionally snow-free sites. In most cases the consequences are only visible after thawing. By then it is very difficult to determine the origin of the damage due to the complexity of stresses occurring in the course of a winter in the mountains. Distinctive frost damage was found at the end of November 1980 in *S. montanum* on a rugged spot at 2400 m a.s.l. In the middle of February 1982 M. Burtscher (pers. comm.) observed a group of *S. montanum* plants (2700 m a.s.l.) on a southward-facing rock. This site had just become snow-free after a warmer period and had frozen overnight. The biggest specimen, which would have flowered during the next summer, was completely dead. Various minor daughter rosettes showed lesser degrees of frost damage on leaves; however, the apex and the stem were undamaged. Due to their excellent regeneration capability *Sempervivum* species can persevere on very exposed growing spots.

Heat damage in the natural habitat

Observations of heat damage to high mountain plants are rarely made and there are hardly any reports looking at heat necrosis of wild plants on their natural site. One reason for that could be that it has not yet been systematically studied (Biebl, 1962, p. 178). Heat damage can only be verified if the plant temperature is controlled throughout the damaging process.

The hottest spots in the Alps are eroded bare patches in the dwarf heath shrub and in alpine grassland. Under clear skies, with dry soil and little wind the patches of bare humus soil in the vegetation gaps can reach high surface temperatures of 50–55 °C or even 60–75 °C (Kronfuss, 1972; Turner, 1958). On the fringe of a closed vegetation, single individuals of the annual plant *Euphrasia minima* grew within the eroded bare patches. We investigated them for heat damage but could not find any. *E. minima*, being a facultative hemiparasitic plant, can draw sufficient water from the surrounding grass roots to perform efficient transpirational cooling. Even with strong solar radiation we recorded average leaf temperatures of only 35 °C. In addition, air turbulence brings about an air exchange within seconds by removing all but a few millimetres of the boundary layer thus improving heat emission (Berger-Landefeldt, 1958).

Cushion plants, especially on sunny slopes, can heat up considerably. In fact, distinct heat damage was observed in *Saxifraga paniculata* at 56 °C at 2200 m a.s.l. (Neuner et al., 1999) and in *Minuartia recurva* at 57 °C at 2600 m a.s.l. (Buchner and Neuner, 2003). Körner (2003, p. 113) reports heat damage to *S. acaulis* cushions at 2600 m a.s.l. to be quite common.

Laboratory tests of frost and heat resistance on different types of mountain plants

Plant species and study sites

The selected high mountain plants represent different growth forms, different geographical distributions, elevation ranges and habitat preferences (Fig. 4).

S. acaulis (L.) Jacq. (Caryophyllaceae) is an arctic-alpine geoelement. In Europe this species can be found in the Pyrenees,

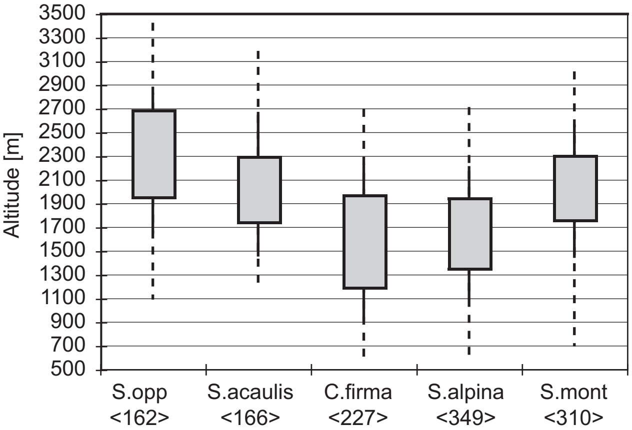

Fig. 4. Elevation range of selected high mountain plants in the Tyrolean Alps: *Saxifraga oppositifolia*, *Silene acaulis*, *Carex firma*, *Soldanella alpina* and *Sempervivum montanum*. The box plots show the 75th and 25th percentiles (margin of boxes), the whisker extends over the range of the 10th and 90th percentiles. *Dotted line*: lowest and highest habitats. Numbers in brackets: number of habitats. According to Polatschek (1999, 2000, 2001a, 2001b).

in the Alps as far as the Carpathians, in the Apennines and in the north western Balkan Mountains. The elevation range of *S. acaulis* in the Tyrolean Central Alps mainly lies between 1700 and 2400 m a.s.l.; but it can be found up to 3200 m a.s.l. (Polatschek, 1999). The dense cushions grow on wind-exposed ridges, of rocky soil and open alpine grassland.

M. sedoides (L.) Hiern (Caryophyllaceae) is a species found in the Alps and southern European mountains with an elevation range between 2200 and 2800 m a.s.l. and an altitudinal limit of 3300 m a.s.l. (Backhuys, 1968). The hard hemispheric cushions grow on rocky slopes and wind-exposed ridges associated with *S. acaulis* and *C. firma*.

S. oppositifolia L. (Saxifragaceae) is a widespread arctic-alpine species with oceanic occurrences. According to Polatschek (2001a) *S. oppositifolia* can mostly be found in the Tyrolean Alps between 1900 and 2700 m a.s.l. (about 60% of the documented cases). The evergreen, flat cushions live on scree in open pioneer communities.

C. firma Mygind (Cyperaceae) is a Central European, endemic high mountain plant whose distribution is limited to the Alps and the Carpathians. This species typically grows in the alpine and subnival zone of the calcareous mountains. In the Northern Alps the plant community of *Caricetum firmae* is characteristically found between 1200 and 2200 m a.s.l. with findings as low as about 800 m a.s.l. due to avalanches and as high as 2700 m a.s.l. (Polatschek, 2001b). This pioneer species prefers growing on nutrient-poor soils, on scree and on rocky swards, on windy ridges and snow-free spots as well as wind-protected areas with strong solar radiation.

Soldanella alpina L. (Primulaceae) is an alpine to sub-mediterranean mountain species. The highest location in the Tyrolean Alps was at 2700 m a.s.l. The vertical distribution ranges from 1300 to 2100 m a.s.l. (Polatschek, 2000). The wintergreen rosette plant is an obligatory chionophyte and grows on moist pastures, on humus soil and in snow-beds. *Soldanella pusilla* Baumg. can be found as low as 900 m a.s.l. in the Tyrolean Alps but is mostly found between 1500 and 2300 m a.s.l. and occasionally as high as 3000 m a.s.l. (Polatschek, 2000).

S. montanum L. (Crassulaceae) is a mid-southern European mountain plant. The elevation distribution ranges from the montane to the nival zone (3250 m a.s.l., Braun, 1913); *S. montanum* is the highest ranging *Sempervivum* species. In the Tyrolean Central Alps this plant can mostly be found between 1800 and 2300 m a.s.l. (Polatschek, 1999). The succulent rosettes prefer dry, warm and shallow soil habitats on open grasslands and rocks. *Sempervivum arachnoideum* L. and *Sempervivum tectorum* L. are also succulent rosette plants ranging from 600 to 2800 m a.s.l. They need warm dry microsites similar to those of *S. montanum*.

Sampling sites

The plant material for the investigations was collected in the Tyrolean Alps at heights between 2100 and 2500 m a.s.l. The majority of the samples were obtained from the Northern Calcareous Mountain range, especially from Mt Hafelekar (47°18′N, 11°23′E, 4 km north of the Inn valley near Innsbruck). Cushions of *S. acaulis*, *M. sedoides* and *S. oppositifolia* were taken from gravel and rocky outcrops on a sun and wind-exposed west-facing slope (25–30° inclination) about 30 m below the peak of Mt Hafelekar. Samples of *C. firma* were collected from a sun- and wind-exposed western slope (18–22° inclination) with little, often no, snow cover in winter and ground frost lasting far into spring. *S. alpina* samples were taken from snow-protected hollows. *S. montanum* samples were collected in the Central Alps on Mt Patscherkofel (47°13′N, 11°20′E, 6 km south of the Inn valley) on south-western slopes between 2000 and 2200 m a.s.l. In order to have a valid comparison to *S. montanum*, S. *arachnoideum* and *S. tectorum* samples were collected from an alpine steppe in a semiarid valley above Latsch and Naturns (Vinschgau, Southern Tyrol) at an elevation between 700 and 800 m a.s.l.

The plant material was collected at defined phenological dates. During winter the sampling had to be carried out under very challenging conditions as the plants had to be chiselled out of the frozen soil. From time to time the study sites could not be reached due to danger of avalanches, which is why only a limited amount of plant material was available. The samples were immediately put into nylon bags (to prevent them from drying out) and brought to the laboratory within two hours.

Resistance tests

In order to obtain ecologically useful results about the temperature resistance of the different plant species it is necessary to carry out a complete investigation programme including the seasonally different resistance levels under the given weather conditions (actual resistance; R_{act}) as well as the maximum and minimum cold and heat resistance. The maximum resistance ($R_{\max}$) is seen as the highest hardening level and the minimum resistance ($R_{\min}$) as the lowest dehardening level.

Freezing treatment

The treatment was carried out in four programme controlled freezers, which could be cooled down to −50 °C and an ultralow freezer (Köttermann; Uetze Hänigsen Germany) which could be cooled to temperatures as low as −80 °C (Cernusca and Larcher, 1970). Fluctuations could be buffered down to 0.2 °C by wrapping the plant parts in aluminium foil and putting them into insulated boxes of 5 cm polystyrene foam. The temperatures were recorded by platinum thermometers (within the samples) and analogue dotted-line recorders (Schenk; Wien Austria).

In the case of *direct cooling* the samples were brought to the target temperature at a cooling rate of $10\,\mathrm{K\,h^{-1}}$; a quick temperature decrease to given target temperatures was used to determine the current frost resistance. *Gradual cooling* was carried out by lowering the temperature stepwise at a rate of 1–$3\,\mathrm{K\,h^{-1}}$ to simulate a natural frost event (Larcher, 1990a, p. 83). In winter, the plants were exposed to the given target temperature for about 10 h, and in summer for between 5 and 6 h. By performing stepwise cooling the hardening capacity of the given plants was determined.

After the frost treatment the samples were slowly defrosted in the closed freezer with an increase in temperature of 3–5 K h^{-1}. The amount of plant material needed depended on the extent of the investigation. For each species at each sampling date, there were 5 (in summer) to 8 (in winter) cooling steps per cooling mode as well as at least 4–5 replicates for each test.

Supercooling treatment

In winter, *S. acaulis* and *S. oppositifolia* were tested for supercooling. A small portion of the cushions was immediately treated with liquid nitrogen (−196 °C) by immersing the samples in test tubes. The test tubes remained in the liquid nitrogen for 12 h. Another portion of the samples was cooled down stepwise in the deep freezer to a temperature of −80 °C over a period of 48 h (according to Sakai, 1960). After exposing the samples to liquid nitrogen for 12 h they were equilibrated at −25 °C and then defrosted.

Heat treatment

Heat treatment was carried out in hot water baths with an accuracy of ±0.1 K (Thermomix Braun; Melsungen Germany). The plant samples were wrapped in adjacent, temperature-resistant and watertight plastic bags (Kalle Bratfolie 2000, Germany). The test temperatures ranged from 42 to 62 °C at temperature steps of 2 K.

Heat damage does not occur linearly but dose-dependently as it increases with rising temperatures and extended exposure (Sapper, 1935). Therefore, the standard exposure time was 30 min with an additional 5 min for temperature adjustment (after Lange, 1965).

Evaluation of damage

After heat and freezing treatment the samples were kept at 15–20 °C in diffuse light and with sufficient water until the actual extent of damage was visible. This took about 2–3 days during the growing season and 1–2 weeks during winter dormancy.

Visual determination of injury

Damage became visible as withering, discoloration and as dried patches. The extent of necrotic patches seen on the leaves was estimated after full development of the symptoms. Necrotic patches on leaves were especially recognizable in transmitted light. Organs had to be cut and examined under the microscope to determine the extent of damage such as tissue decay and discoloration.

Tetrazolium test (TTC)

In order to determine tissue damage, especially in meristems, a viability test was carried out with the help of the redox indicator 2,3,5-triphenyltetrazolium chloride (Fluka Chemie; Buchs, Switzerland). Dehydrogenase activity reduces the colourless tetrazolium salt to red-coloured triphenyl formazan. In the case of a positive reaction the viable cells appear red (Ruf and Brunner, 2003; Stattin and Lindström, 1999). The topographic tetrazolium test (Lakon, 1942) was carried out according to Larcher (1969, 1990b): after a period of 5–10 days buds, parts of the stems and underground organs were immersed in a 0.5% TTC solution (solvent: phosphate buffer; pH 7–8) in closely sealed glass tubes. The 1–2 cm long pieces were cut with a razor blade to allow the reagent to enter. Samples where the reagent had difficulty entering were placed under reduced pressure to remove air from the intercellular spaces and to support the infiltration of the TTC buffer. If necessary the reagent was charged with the broad-spectrum antibiotics Gentamicinsulfat (Serva Nr. 22185, Heidelberg) at a concentration of 40 μg/l to inhibit the growth of soil bacteria in the various plant parts. The airtight sealed tubes were incubated in the dark at 25–30 °C for 24 h. After the incubation period the samples were rinsed with water and tested immediately.

Trials for regenerative capacity

If damage could neither be determined through visual observation, nor by the TTC test, the regenerative capacity of shoots was measured over several weeks. Unfortunately, at that time ongoing cultivation of the plants was not possible; but sprouts could be observed in the laboratory over the next 2–3 weeks.

Assessment of damage

The extent of damage was identified for different organs and tissues (buds, leaves, apices, stems, rhizomes and roots). The relevant measure of damage depends on whether ecological or physiological questions are the focus of attention: the temperature at which damage first occurs gives valuable data about risks to the plants in their natural environment. Fifty percent tissue damage is seen as a physiological standard. If important parts of the plant, regenerative buds and rhizomes in particular, are severely damaged the plant can no longer survive. The following threshold values for injury were distinguished:

LT_o = the lowest temperature without necrotic damage,
LT_i = initial injuries,
LT_{50} = temperature that causes damage to 50% of tissue (half damage),
LT_{100} = only a few tissues survive or complete damage.

Leaves show visually distinct damage symptoms. It turned out to be a lot more difficult to assess LT_{50} for buds and stems. We did not want to use any all-inclusive values (e.g. conductivity methods) for whole plants due to the heterogeneity of the tissues. However, the thresholds of injuries (LT_i and LT_{100}) as well as easily detectable damage ranging from slight (<50% lethality) to heavy (>50% lethality) losses could be defined with high accuracy. LT_{50} was calculated by using interpolation with a sigmoid function (Fig. 5).

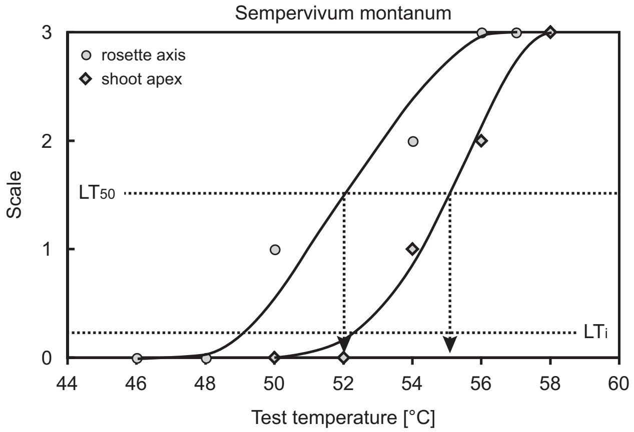

Fig. 5. Example for the determination of LT_{50} heat damage (*arrows*) using a logistic sigmoid function (P-Fit Biosoft, Durham, USA). Scales: uninjured tissues (0), less than half damage (1), more than half damage (2) and complete mortality (3). Sample size *n* = 7–9.

Results

Silene acaulis (L.) Jacq. and Minuartia sedoides (L.) Hiern

S. acaulis and *M. sedoides* are compact cushion plants that grow on rocks and coarse gravel. *S. acaulis* also occurs as a flat cushion in alpine grassland and on humic soil. Both species can survive the winter on snow-free sites. In the case of *S. acaulis* vegetative proliferation starts in May and June. The flowering period is site dependent and lasts from June to the beginning of August. Until autumn the majority of the small leaves on the short-stem shoots die and only the innermost shoot apices remain green over the winter. *M. sedoides* blossoms in summer between July and August.

Seasonal changes in frost resistance (Fig. 6)

In the late winter of 1971 there was a series of severe frosts. Only in April and May did warmer spring temperatures start. The growing period was chilly at first, however, the summer (July and August) and the autumn were very warm. The winter in 1971/1972 was exceptionally mild, spring was very cool with regular night frosts until June. In the summer of 1972 several sudden falls in temperature occurred with light frost and snowfalls; colder periods were also very frequent in autumn.

The annual course of the actual resistance levels (R_{act}) of *S. acaulis* reflects the phenological phases and the changing weather conditions. From April 1971 onwards the sharp reduction in frost resistance marked the onset of developmental activity. During the onset of the sprouting in May all plant organs dehardened but were able to reharden quickly in case of late frosts. Maximum frost sensitivity (LT_{50} of −6 to −7 °C) was only reached in July and continued until the completion of growth in August. In comparison, Taschler and Neuner (2004) measured an LT_i value of -6.0 ± 0.3 °C of leaves under field conditions in 2000 m a.s.l. in summer.

The hardening phase in autumn stretched over a longer period. When leaflets turned yellow in September and October the frost resistance of the shoots and roots ranged between −10 and −30 °C. In November all plant organs were only partly damaged by temperatures as low as −30 to −35 °C. Only in January did *S. acaulis* reach the winter peak of frost resistance. In winter a wide distribution of resistance values could be observed. Most cushions were damaged after a treatment with temperatures of −60 to −65 °C. On the other hand, several samples also survived −80 °C. In this state of maximum winter hardiness these rock plants can also survive on windy and snow-free ridges.

The frost resistance of *M. sedoides* was only investigated once in winter and once in midsummer and showed the same resistance values as *S. acaulis*.

Maximum frost resistance after hardening

During winter all plant organs and tissues of *S. acaulis* and *M. sedoides* were equally resistant to frost. Maximum resistance values (R_{max}) were obtained through stepwise cooling. The plants survived the lowest temperatures (−80 °C) even dipping into liquid nitrogen (−196 °C) (Table 2). The plants did not lose their deepest hardening ability even when they were exposed to freeze–thaw cycles.

During sprouting the terminal buds and young shoots were the most sensitive organs of the plant (−8 °C) when undergoing stepwise cooling. The lateral buds were significantly more resistant (−15 °C) than terminal buds and could therefore take over repair functions. The bark and the cambium of stems as well as the roots turned out to be 5–10 K more resistant than the current frost resistance.

During summer, the shoots were as frost resistant when cooled directly as when cooled stepwise which means that stepwise cooling (18 h) does not induce an increase in resistance. However, a 3-day long cold pre-treatment of −2 to +4 °C under short-day conditions brought about an increase in resistance in leaves from −7 to −10 °C. The stems of a few resistant *S. acaulis* and *M. sedoides* individuals endured temperatures of −20 °C even in summer and were 10 K more resistant than the leafy shoots.

An additional 3-day long cold treatment under short-day conditions induced a further 5 K increase in resistance in the underground parts of the plants. In September and October the hardening ability was especially high; over a short period of time resistance values of −30 °C were reached.

Dehardening through heat treatment in winter

Above-zero temperatures cause a loss of frost resistance. Even in mid-winter exposure to warming may be sufficient for plants to lose most of their hardening within a couple of days. During

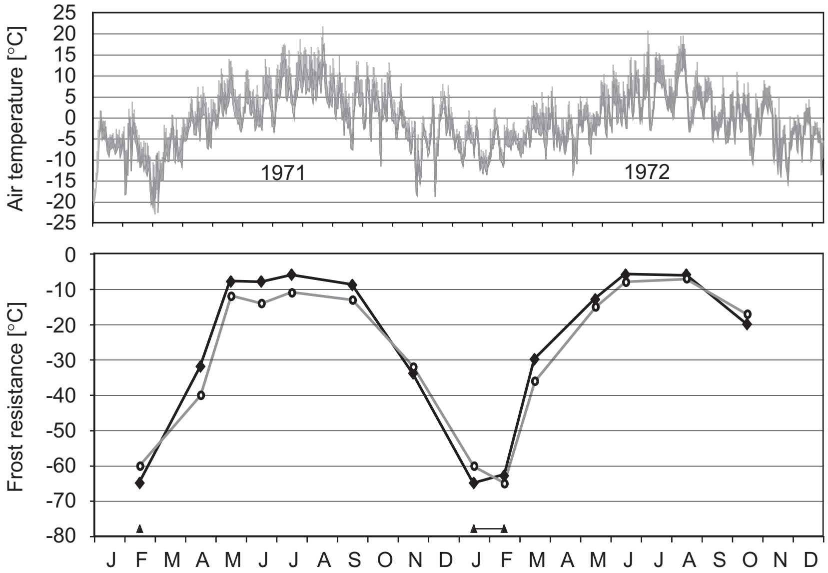

Fig. 6. Annual changes of air temperatures on Mt Patscherkofel (2247 m a.s.l.) and seasonal variation in frost resistance of *Silene acaulis* in 1971 and 1972. Actual freezing resistance of (◆) shoots and (○) roots; (▲) high tolerance of shoots achieved by stepwise frost hardening. LT_{50} = temperatures causing 50% frost damage.

Table 2
Frost and heat resistance of *Silene acaulis*.

	Winter dormancy Dec–Feb	Dehardening March+April	Sprouting May+June	Growing period July+Aug	Hardening Sept+Oct
Frost resistance					
Ract					
Shoots	−60 to −65	ca −30	−8 to −13	−6 to −7	−10 to −20
Roots	−60 to −65	−35 to −40	−12 to −15	−6	−13 to −17
Rmax					
Shoots	−80 [−196]	−40		−7 (−10)	
Foliated shoots			−8 (−15)	(−10)	−30
Stems (cambium)	−80 [−196]	−65 to −70	−18 to −32		−30
Roots (cambium)	−80 [−196]	−55 to −80	−18 to −30	−15 (−23)	−35
Rmin					
Shoots	−40			−6	
Roots	−50			−6	
Heat resistance					
Rmax					
Shoots	58			54	58
Stems (cambium)	58				
Roots (cambium)	60			53	57
Rmin					
Shoots	52[a]/54		52	52	54
Stems (cambium)	56				
Roots (cambium)	54		50	52	

Temperatures (°C) causing 50% injury. R_{act} actual frost resistance; R_{max} highest resistance after hardening; R_{min} minimum resistance in the dehardened state. Accuracy of values: 1–3 K. Values in brackets refer to single samples.

[a] Snow covered.

winter dormancy, hardiness to frost of *S. acaulis* was investigated after a 3–4 day long pre-treatment at room temperature. The leafy shoots of thermally treated plants showed an LT_{50} of −40 °C in January and of only −25 °C in February. The underground parts of the plant were not fully damaged by temperatures of −50 °C. The dehardening effect brought about by warming was not as effective as on aboveground organs.

Seasonal changes in heat resistance

Heat resistance of *S. acaulis* changed, just like frost resistance, in the course of a year depending on activity status and dormancy. During the period of intensive growth the underground parts were most sensitive to heat (Table 2). During midsummer the resistance differences between the investigated individuals and between different organs were very small. However, there were large differences between different individuals in autumn and winter: the highest resistance values recorded were 58–60 °C, the lowest 52–54 °C. In a comprehensive summer data series, which was collected with modern instruments at field sites in the Central Alps (1950–2600 m a.s.l.) the range of heat tolerance limits of leaves of *S. acaulis* was between 45.5 and 54.5 °C (LT_{50} mean 50.3 ± 1.9 °C; Buchner and Neuner, 2003; Neuner et al., 2000).

Saxifraga oppositifolia L.

S. oppositifolia is a prostrate cushion with evergreen shoots. It grows on rocks and moraine soil. The cushions survive winter under the snow but also on windblown and sparsely snow-covered sites. Flowering of *S. oppositifolia* lasts from May until the end of June depending on the growing location.

Seasonal changes in frost resistance (Fig. 7)

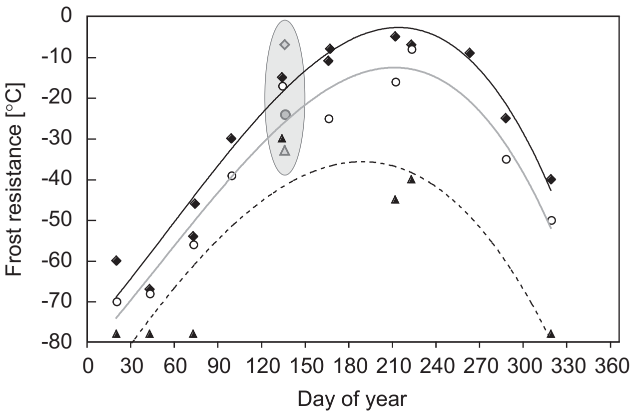

Fig. 7. Seasonal variation in frost resistance of *Saxifraga oppositifolia.* Data were acquired between October 1970 and January 1973. Actual freezing resistance of (◆) shoots and (○) roots; (▲) high tolerance achieved by stepwise hardening to frost. Temperatures causing 50% frost damage (LT_{50}). *Ellipse*: frost resistance at onset of growing in May1971 (*grey symbols*) and May 1972 (*black symbols*).

The seasonal dynamics of the actual frost resistance of *S. oppositifolia* is marked by a very large increase in frost hardening during winter, a sudden decrease of resistance during flowering time in May and parts of underground organs hardened all year round.

The winter experiments showed an individual distribution of resistance values. Leaves and leafy shoots had LT_{50} values between −60 and −67 °C, and roots about −70 °C. After snowmelt in May, a quick dehardening of all plant organs could be observed. This phase coincided with the opening of flower buds. Before the summer, resistance decreased by a few degrees: the annual minimum frost resistance of new shoots was between −6 and −7 °C; of roots between −8 and −15 °C. However, the underground organs of some individuals were frost resistant down to −55 °C during the growing season. Shoots of *S. oppositifolia* measured *in situ* in summer had a mean LT_{50} of −7.8 ± 0.2 °C, and thus were on average frost hardier by 1.1 K (± 0.2 SE) than in laboratory tests (Taschler and Neuner, 2004).

Maximum frost resistance after hardening

During winter *S. oppositifolia* was absolutely insensitive to low temperatures after undergoing stepwise cooling. Neither temperatures of −80 °C nor dipping into liquid nitrogen (−196 °C) could damage the plants. The maximum frost hardiness remained constant over the course of the winter. Even short-term exposure to changing freezing conditions did not bring about a dehardening effect.

After winter dormancy the decrease of resistance started as active growth began in May. During the peak growing season in summer the leaves froze at −8 °C, the shoots and underground parts between −18 and −25 °C when undergoing stepwise cooling (Table 3). In the shoots all the different tissues were equally hardy, in the underground parts of the plant, however, the cambium and the bark tuned out to be more resistant than the xylem. Stolons and taproots of single individuals also remained extremely hardy throughout the summer. A possible explanation for this is that these tissues are dormant despite being part of actively growing cushions. The fact that different parts of a plant are not always in the same developmental stage is shown by latent buds of woody plants in summer.

Dehardening through heat treatment in winter

Plants, which were collected from their natural growing location in January and were kept under warm conditions (constant room temperature of about 20 °C, long-day lighting) for a few days before frosting, were less frost hardy. In the case of direct frosting the shoots only endured temperatures of −20 to −25 °C, and underground organs temperatures of −25 to −50 °C. However, in the case of stepwise frosting rehardening took place in which shoots reached resistance values of −30 to −45 °C; the underground stems reached values of −45 to −60 °C. The relatively broad distribution of the individual resistance values points out that not all cushions deharden and reharden at the same speed.

Seasonal changes in heat resistance

From the onset of the growing season until midsummer *S. oppositifolia* was highly heat resistant (Fig. 8). The leaves and the buds (51–52 °C) were more resistant than the shoots (50 °C) and the roots (46–48 °C). During autumn the heat resistance increased by 1–2 K. In winter broad individual distributions of resistance values were measured. Within cushions, which had reached a high resistance level, the shoots above the soil surface were tolerant with an LT_{50} value of 58 °C; within cushions with a low resistance level the roots (48 °C) were more sensitive just like in the summer. These two patterns could have been caused by differences in the snow cover. Individuals without snow cover were more resistant because of frost drying than individuals that were supplied with water under the snow.

Carex firma mygind

C. firma is the only true cushion plant among the European graminoid tussocks (Rauh, 1939). The numerous leafy shoots grow out of rhizomes; the strong roots stemming from the shoots are adventitiously shallow rooted. On the southward-facing collection sites the vegetative shooting started in June and the main shoot growth lasted until the beginning of August. By October the outermost leaves of the rosette-like shoots had died except for the youngest leaves in the middle.

Seasonal changes in frost resistance (Fig. 9)

The winter state with the lowest actual frost resistance was only reached at the beginning of January. The LT_{50} values of leaves were as low as −45 °C; of rhizomes as low as −65 °C. This level of resistance was maintained until the middle of March. Dehardening was delayed until May. The most frost-sensitive phase lasted from the beginning of June until the end of August. During the summer the leaf blades froze at −7 °C and the leaf sheath at −6 °C. Frost damage within the intercalary growing areas resulted in death of all leaves. During summer young plants showed a similar sensitivity to frost as adult plants and could be cooled down to a temperature of -7 ± 1.4 °C without freezing (Cernusca and Vesco, 1976).

Maximum frost resistance after hardening

Stepwise cooling during winter increased the frost resistance of leaves by about 25 K more than direct cooling (Table 4). The leaf blades and leaf sheaths were most resistant during winter (−70 °C). At the time of their maximum frost resistance shoots as well as rhizomes showed a much higher safety margin, which is hardly ever exploited on the natural growing location. Among the tissues of the rhizome the bark was most resistant; followed by the xylem and parenchyma, which were a bit more sensitive. From June onwards and over the period of the whole summer the leaves showed almost no hardening potential with the rhizomes being significantly more resistant. However, towards the end of August a slight hardening effect could already be traced in all organs. In the middle of November none of the plants had reached their maximum frost resistance yet.

Table 3
Frost resistance of *Saxifraga oppositifolia*.

	Winter dormancy Dec–Feb	Dehardening March+April	Sprouting May	Growing period July+Aug	Hardening Oct
Ract					
Shoots	−60 to −65	−45 to −55	−7 to −15	−6 to −7	−25
Roots	−70	−40 to −55	−17 to −25	−8 to −15	−35
Rmax					
Leaves	−80 [−196]	−45 to −60	−13 to −24	−8	−30 to −80
Stems (cambium)	−80 [−196]	−45 to −60	−32 to −60	−18 to −25	−80
Roots (cambium)	−80 [−196]	−45 to −60	−35 to −70	−18 to −25	−50 to −80
Roots (xylem)				−16 to −22	
Rmin					
Leaves	−30 to −45			−5	
Stems (cambium)				−16 to −17	
Roots (cambium)	−45 to −60			−18	

Temperatures (°C) causing 50% injury. R_{act} actual frost resistance; R_{max} highest resistance after hardening; R_{min} minimum resistance in the dehardened state. Accuracy of values: 2–3 K.

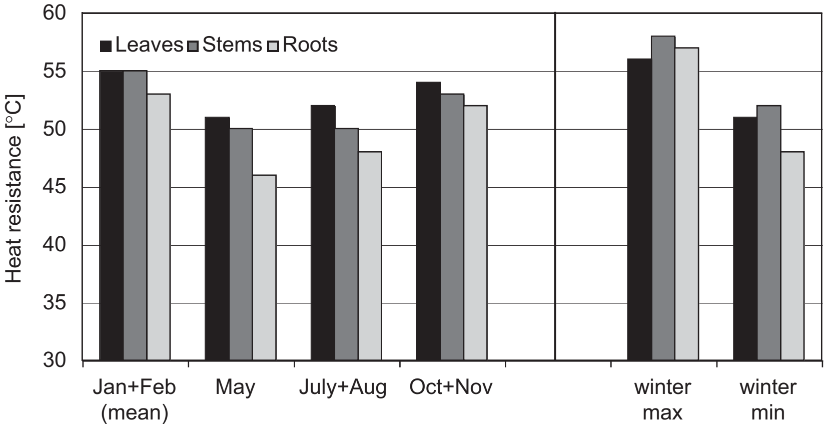

Fig. 8. Seasonal variation in heat resistance of *Saxifraga oppositifolia*. LT_{50} = temperatures causing 50% damage. *Right*: differences in heat resistance of individual cushions in winter: (*max*) high tolerance, (*min*) low resistance.

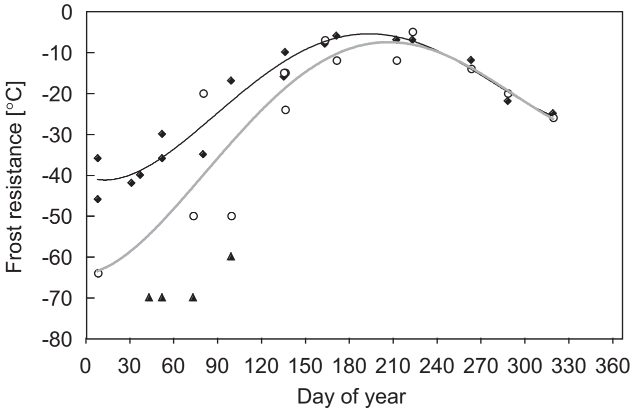

Fig. 9. Seasonal variation in frost resistance of *Carex firma.* Data were acquired between October 1970 and January 1973. Actual freezing resistance of (◆) shoots and (○) rhizomes; (▲) high tolerance achieved by stepwise hardening to frost. Values are temperatures causing 50% frost damage (LT_{50}).

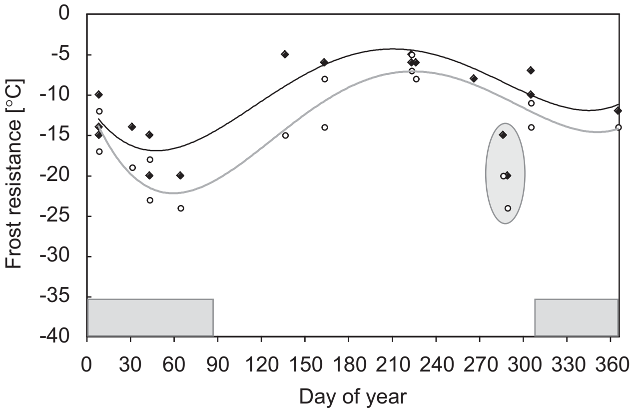

Fig. 10. Seasonal variations in frost resistance of *Soldanella alpina.* Data were acquired between October 1970 and January 1973. Actual freezing resistance of (◆) shoots and (○) rhizomes. LT_{50} = temperatures causing 50% damage. *Grey areas*: winter snow cover. *Ellipse*: early frosts in October in 1972.

Table 4
Frost resistance of *Carex firma*. Temperatures (°C) causing 50% injury.

	Winter dormancy Dec–Feb	Dehardening May	Growing period June–Aug	Hardening Oct+Nov
R_{act}				
Leaves	−35 to −45	−10 to −15	−6 to −7	−22 to −25
Rhizomes	−50 to −65	−12 to −25	−7 to −12	−20 to −26
R_{max}				
Leaves	−70	−15	−7 to −8	−35
Rhizomes	−70	−15 to −25	−10 to −15	−30
R_{min}				
Leaves	−25 to −35			
Rhizomes	−30 to −50			

R_{act} actual frost resistance; R_{max} highest resistance after hardening; R_{min} minimum resistance in the dehardened state. Accuracy of values: 1–2 K (summer), 2–3 K (winter).

Dehardening through heat treatment in winter

In the course of a 5-day long heat treatment in January the frost resistance of the leaves decreased to −25 °C and the resistance of rhizomes to −30 °C. In February the dehardening effect proved to be more effective resulting in resistance values for all organs of −12 to −14 °C. Formerly heat-treated plants could not be rehardened by stepwise cooling.

Seasonal changes in heat resistance

The resistance level in *C. firma* remained constant throughout the year. The LT_{50} values of leaves ranged from 58 to 60 °C; for rhizomes it was around 60 °C. Only during the onset of the growing season did the resistance values decrease. During this phase the LT_{50} values of leaves were between 54 and 56 °C; of rhizomes between 54 and 57 °C. Differences in resistance between the individual tissues could only be traced during the onset of the growing season and concerned the bark of the rhizomes (2 K more sensitive than the remaining tissues). In contrast to frost resistance there was no difference between heat resistance in the leaf blade and the leaf sheath.

Soldanella alpina L.

This evergreen rosette plant grows on humid and clayey soil of rough grassland and depressions. The leaves need snow cover between November and May. The plagiotropic rhizomes are thermally protected by litter throughout the year.

Seasonal changes in frost resistance (Fig. 10)

While plants are actively growing, beginning in April or May and lasting until the end of August, the frost resistance remains low. During the growing season, leaves suffered from damage at temperatures of −5 to −6 °C; rhizomes at −8 °C. The resistance values after direct cooling did not differ from stepwise cooling.

Maximum resistance was first observed in autumn before the first snowfall. During a cold spell in October in 1972 a quick hardening to temperatures of under −15 °C occurred as result of a series of days with minimum air temperatures of −6 °C. Following heavy snowfalls frost resistance decreased again. In February and during the first week in March a second peak of frost resistance occurred in leaves (−20 °C) and rhizomes (−24 °C).

Hardening through cold treatment

In November 1971 a few specimens of *S. alpina* were conditioned in the dark for 4 days in a refrigerator (−8 °C) after they had been covered by snow for 2 weeks at their natural growing location. These plants were fully intact after the treatment. A following stepwise cooling resulted in an increased resistance: 2 K (in leaves) and 4 K (in rhizomes). During midsummer samples of *S. alpina* were kept for 5 days in a cooling chamber (−2 to +4 °C) under short-day conditions (8 h light, 16 h darkness). This cold treatment under short-day conditions led to an increase of frost resistance in rhizomes by 4 K; the leaves, however, did not turn out to be hardier.

Seasonal changes in heat resistance

The highest level of heat resistance of *S. alpina* was reached in late winter. The winter value of heat resistance (LT_{50}) was 57–58 °C in leaves and 54–57 °C in rhizomes, even though the plants were covered by snow throughout the winter. During summer the LT_{50} of leaves was between 52 and 54 °C; and of rhizomes was 55 °C. A gradient between resistances in different tissues could only be observed once in October: at that time the bark of the rhizome was more sensitive (2 K) than the rest of the tissues. Apart from that there were never any differences in resistance measured within the organs.

Sempervivum species

The alpine *Sempervivum* species grow on xerothermic microsites. During winter they need to be covered by snow, but not for longer than 7 or 8 months and can therefore be classified as semichionophilous (Larcher and Wagner, 1983). The main growing period takes place in spring (May and June) whereas the flowering period lasts from July until September.

Frost resistance of Sempervivum montanum

During summer the first necrotic spots could be found on leaves exposed to −5 °C; at −6 to −7 °C half of the rosettes were frozen, and finally at −8 to −9 °C all the plants were dead (Fig. 11). The outermost leaves were most sensitive, whereas the innermost and young leaves with the apex and the axis coped better with the frost. All in all there were almost no differences in resistance between the different plant organs; it was only the main root that was less susceptible by 1 K. After a 3-day long cold treatment of *S. montanum* at a constant 0 °C (day and night) the freezing point in leaves was lowered to −5 °C. Ice nucleation in tissues during summer is not necessarily lethal. In a follow-up experiment, plants of *S. montanum* were kept near 0 °C in a cooling chamber for one day and then were gradually cooled down. At −2.3 °C the rosettes were frozen, the leaves had a glassy appearance, and the CO_2 uptake had ceased. After thawing at +5 °C, the infiltrates were gone within one day and the photosynthetic process was reactivated (Wagner and Larcher, 1981).

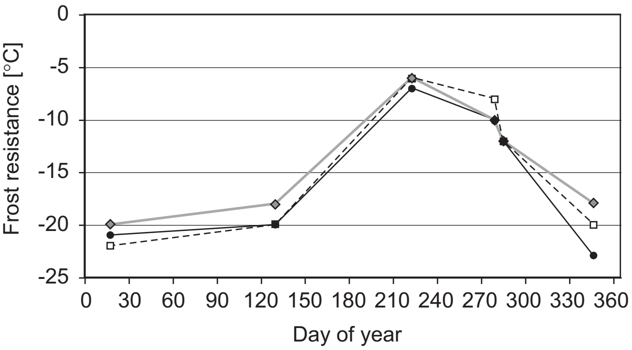

Fig. 11. Seasonal variations in frost resistance (50%) of *Sempervivum montanum:* Data were acquired between 1973 and 1974. Values of (●) apex and innermost leaves of the rosette, (◆) outermost leaves of the rosette and (□) short stem.

In the first week of October the rosette leaves and the apex endured temperatures of −9 °C without damage, at −12 °C they were totally frozen. Underground organs (lower rosette axis and main root) showed slight frost damage at −7 °C; at −10 °C however, they were fully damaged. During a series of days with subzero temperatures in the middle of October hardening occurred within 6 days. During winter (air temperatures of −10 °C) snow-free plants had a high degree of hardiness. The apex and the innermost and outermost rosette leaves endured temperatures of −20 °C without suffering any damage. Vegetative daughter rosettes even withstood temperatures of −25 °C.

Heat stress and heat resistance of three Sempervivum species

Heat stress in the mountains never occurs abruptly – it develops during the summer in the course of a spell of fine weather and only when soil is at least superficially dry. For *S. montanum*, water shortage is hardly a limiting factor in the humid regions of the northern Central Alps. On Mt. Patscherkofel the minimum soil water potential measured over several vegetation periods was −0.1 MPa (Cernusca, 1976). At most, the water supply of *S. montanum* was slightly affected during 2–3 week-long dry periods in midsummer.

On the contrary *S. arachnoideum* and *S. tectorum* are affected by regular and week-long heat and drought due to the continental climate at their growing location in the southern Central Alps (Larcher et al., 1989). On steep and southward-facing slopes in semiarid valleys maximum summer temperatures reach 35–38 °C above the vegetation, 50–56 °C on rosette plants under dry conditions (Huber, 1935) and 55–56 °C at the soil surface (Otto, 1974).

Seasonal changes in heat resistance of S. montanum (Fig. 12). During the growing and the flowering period rosettes with an adequate water supply and not heat adapted first showed heat damage at 50 °C. The apex together with the innermost leaves of the rosette were more resistant (LT_{50} values: 54–55 °C) than the outmost leaves and the axis of the rosette. Likewise the flowers and the stem of the inflorescence were more susceptible (Table 5). During the growing season heat resistance values remained approximately the same while temperatures were equable and precipitation was sufficient. Only after night frosts in autumn and the formation of a snow cover in winter did the resistance decrease considerably. In November and December, if a constant snow cover had not yet formed, a brief increase in heat resistance developed.

Maximum heat resistance only developed when solar radiation and temperatures were high and water content low (Fig. 12; summer maximum). During a hot period in August of 1973 rosette leaves could survive temperatures of 52–53 °C without any damage and temperatures of up to 55–57 °C with half damage. At that time the highest temperatures measured in the rosettes were up to 50 °C (see Fig. 3). This extreme overheating of *Sempervivum* species is a result of the plants succulence: the fleshy leaves accumulate heat and emit it more slowly to the

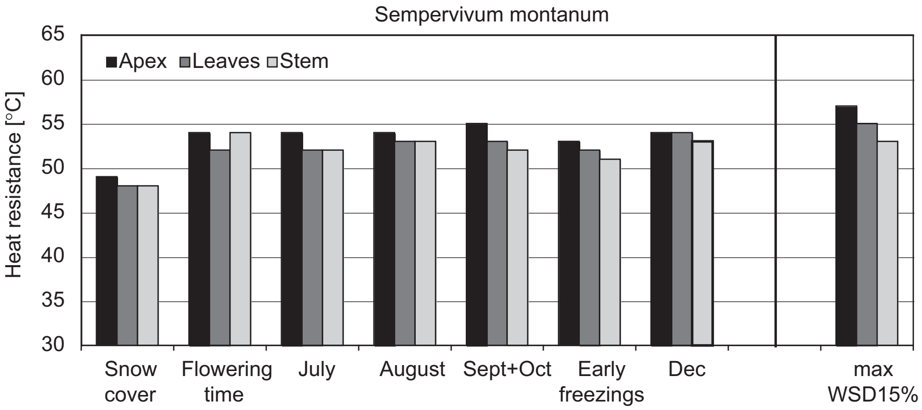

Fig. 12. Seasonal heat resistance (°C) of *Sempervivum montanum*. LT_{50} = temperatures (°C) causing 50% damage. *Right*: summer maximum at 15% water saturation deficit.

Table 5
Heat resistance (°C) of inflorescences of *Sempervivum montanum* in July.

	LT_0	LT_{50}	LT_{100}
Inflorescence stem	48	*50*	53
Buds K	48	*50*	52
Buds C	48	*50*	52
Buds A	46	*47*	52
Buds G	48	*49*	52
Sepals K	50	*51*	53
Petals C	48	*50*	52
Androeceum A	46	*48*	52
Gynoecium G	50	*52*	54

LT_0: highest survived temperatures without damage, LT_{50}: half damage calculated by interpolation; LT_{100}: single cell groups survived.

surroundings due to a smaller surface area and low rates of transpiration cooling.

Seasonal changes in heat resistance of S. arachnoideum and S. tectorum (Figs. 13 and 14). In the rock steppe of Vinschgau in 1975/1976 the two *Sempervivum* species started growing at the beginning of May; the main flowering took place between the middle of May and June. During the hot and dry months of July and August the development of *S. arachnoideum* and *S. tectorum* remained stagnant until sufficient rain in autumn allowed a second short active growth period. During mild winters the air temperature minima ranged from +2 to −5 °C on the mostly snow-free slopes with rare frosts of down to −10 °C. During this season as well as during the humid autumn the heat resistance values of both *Sempervivum* species were at their lowest. In July 1976 (hottest period) maximum heat hardening was reached. In both *Sempervivum* species LT_{50} values of rosette leaves rose to 64 °C; of taproots to 60 °C. The difference between heat resistance in fully hardened and non-hardened plants was 8–9 K in *S. arachnoideum* and 7–8 K in *S. tectorum*.

Increase in resistance can also be induced by desiccation. In an experiment on the effects of droughts carried out by Gamper (1976) *S. tectorum* plants were water-saturated between the middle of July and the beginning of August then allowed to dry out. The individual rosettes ($n = 120$) were treated in the laboratory at 25 °C under diffused bright light. After 10 days the heat resistance was determined. A 29% water saturation deficit led to an increase in resistance of 1–2 K; while a 43% water saturation deficit increased resistance by 2–3 K. This experiment on *S. tectorum* proved that drought has the same heat resistance enhancing effect as heat.

Diurnal adaptations of heat tolerance. Sempervivoideae – being CAM plants – show a distinct diurnal pattern in acid levels as well as fluctuations in heat tolerance (Lösch and Kappen, 1983). The fluctuations of heat resistance depend on the level of warming during the day. The investigated *Sempervivum* species showed a barely discernable increase of 1 K in the course of the day under chilly conditions and cloudy skies. With bigger temperature fluctuations in the course of the day the heat tolerance increased by several degrees centigrade within hours. Therefore, on a hot midsummer day in August the heat tolerance in *S. montanum* was 4 K higher than that measured in the morning (Fig. 15). On this day the leaf temperatures of the rosette were 5 °C in the morning and 47 °C at noon. On sunny days the heat tolerance of *S. arachnoideum* and *S. tectorum* in the afternoon was 2–3 K higher than in the morning.

Discussion

Frost survival of high mountain plants

In the Alps air temperatures above the timberline can sink to −30 °C in winter (Table 1). Rock plants, cushion plants, and tussocks in particular, have temperatures similar to air temperatures and thus show a correspondingly high frost resistance. Therefore, *S. acaulis*, *M. sedoides* and *S. oppositifolia* are fully hardened during winter (LT_{50} of under −80 to −196 °C). *C. firma* also shows a high frost tolerance (LT_{50} −70 °C). These hardy plants possess a safety margin of at least 5–10 K (shoots) and 10–20 K (roots). Plants show a safety margin if their potential (maximum) resistance levels are higher than their actual resistance levels. Under snow cover the microsite temperatures remain between 0 and −5 °C; they rarely fall to −10 °C. Under these conditions snow-protected plants like *S. alpina* and *S. pusilla*, as well as *Sempervivum* species can survive perfectly with a maximum frost resistance of −20 to −25 °C and a safety margin of 10 K (leaves) to 15 K (rhizomes). Only during short winters with little snow are chionophilous plants like *Sempervivum* species endangered as they have only a small safety margin (5 K). This resistance type is frequently found among herbaceous plants in temperate zones, as well as in the lowlands (Sakai and Larcher, 1987; Yoshie and Sakai, 1981a).

Frost resistance as well as hardening capability are linked to the vegetative developmental stages. In addition rapid changes in atmospheric conditions over a season can lead to quick, short-term adaptations and variation in resistance levels. Therefore, injury data are always only approximate values. During spring and autumn the leaves together with the aboveground organs show a wider safety margin and can thus adapt within hours to a sudden fall in temperature. The minimum frost resistance coincides with the growing period when most herbaceous plants are most susceptible. Temperatures of −5 to −8 °C suffice to damage leaves

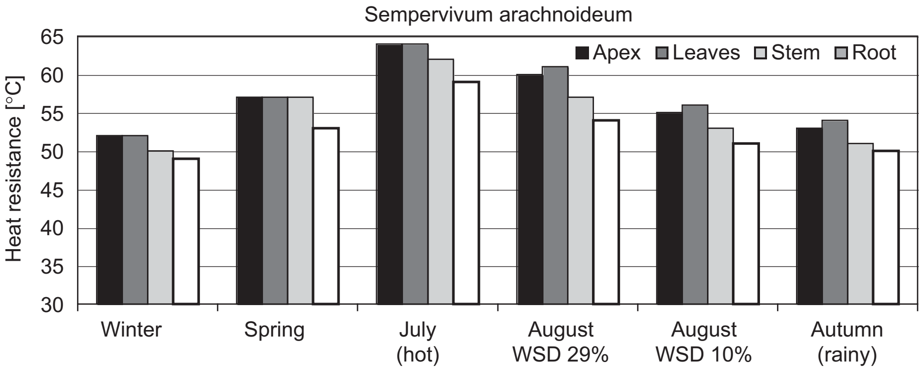

Fig. 13. Seasonal heat resistance (°C) of *Sempervivum arachnoideum*. Data were acquired between 1975 and 1976. *WSD* [%] water saturation deficit. After data by Gamper (1976).

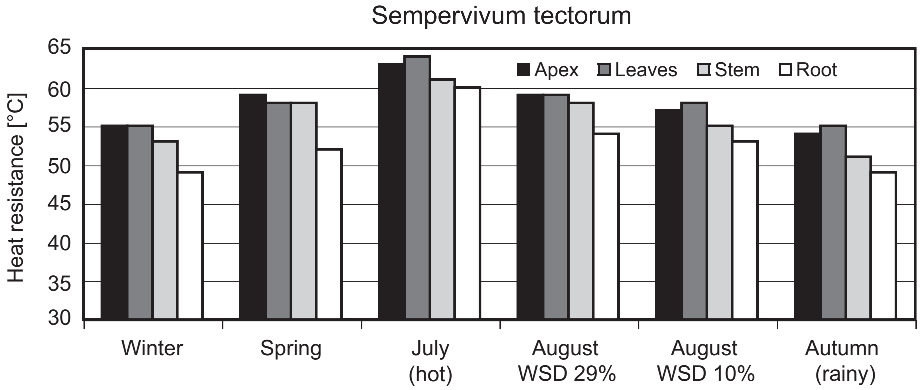

Fig. 14. Seasonal heat resistance (°C) of *Sempervivum tectorum*. Data were acquired between 1975 and 1976. *WSD* [%] water saturation deficit. After data by Gamper (1976).

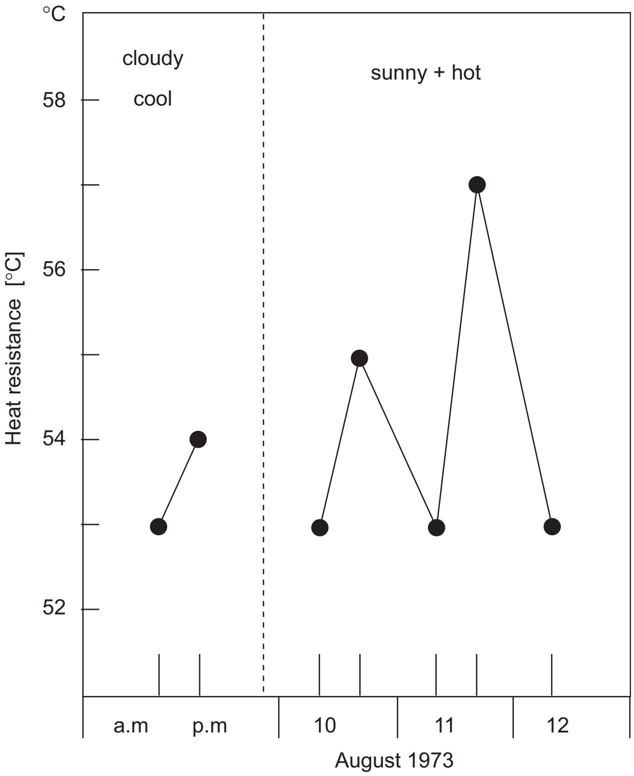

Fig. 15. Diurnal fluctuations in heat resistance of *Sempervivum montanum* during cloudy and cool weather and during a sunny and hot period in August: (*a.m*) before noon and (*p.m*) after noon.

and young shoots. Only a few graminoids are frost hardier during their growing period; for example *Juncus trifidus*, *Carex curvula*, *Nardus stricta*, *Phleum alpinum* (LT_{50}-values of −9 to −11 °C) and *Poa alpina* (LT_{50}-values to −15 °C; Taschler and Neuner, 2004).

The most dangerous temperature events are summer frosts, which occur in the alpine altitudinal zones (−5 to −7 °C) and in glacial regions (−8 to −10 °C). Under ideal conditions cushion plants show a safety margin of about 3−5 K (stems of *S. acaulis* and rhizomes of *C. firma*) and about 10 K (stems of *S. oppositifolia*). Rosette plants hardly ever possess a safety margin. However, frost damage can be repaired by regeneration. *Sempervivum* species can fully renew their leaves as long as the vegetative apex and the stem remain undamaged. If the vegetative apex also dies, recovery takes place through surviving organs such as buds and regenerative tissues. Surviving stolons or more resistant minor rosettes can also induce regeneration.

In Japanese mountains the resistance levels of mountain plants in their growing period also ranges from −5 to −7 °C (Sakai and Otsuka, 1970). The leaves of European and American arctic-alpine species from higher latitudes survive summer frosts of between −4 and −9 °C (Biebl, 1968; Junttila and Robberecht, 1993; Körner and Alsos, 2009; Robberecht and Junttila, 1992). Yoshie and Sakai (1981b) found leaf buds and rhizomes of perennial herbaceous arctic plants that survive −10 and −15 °C in August. During the growing season in arid zones in East Pamir (3860–4760 m a.s.l.) *Primula pamirica*, *Saxifraga hirculus*, *Androsace akbaitalensis* and several Asteraceae, as well as *Stipa glareosa* and *Carex* species survive night frosts of −10 to −20 °C (Tyurina, 1957). Those species were found stiffly frozen in the morning but came back to life after thawing.

Heat survival of high mountain plants

The maximum values (LT_{50}) of heat resistance of *S. arachnoideum* and *S. tectorum* growing at xerothermic locations ranged from 62 °C (stems) to 64 °C (apex). *S. montanum* can also survive temperatures of up to 58 °C in the upper alpine altitudinal zone. Thus, these species are some of the most heat-resistant herbaceous dicotyledons. Graminoid tussocks are also very heat tolerant: shoots and rhizomes of *C. firma* are only damaged by temperatures greater than 60 °C. *C. humilis* growing in the southern Central Alps can also tolerate high temperatures of 59 °C (leaves) and 65 °C (rhizomes) (Larcher et al., 1989). In July on Mt. Patscherkofel (2200 m a.s.l.) leaf temperature tolerance (LT_{50}) of *C. curvula* reached values of 53.6 ± 0.9 °C tested with the help of mobile heat treatments (Buchner and Neuner, 2001). In the present study, *S. acaulis* reached maximum LT_{50} values of 58 °C in shoots and 60 °C in roots. Some *Saxifraga* species turned out to be equally resistant: maximum LT_{50} values measured in *S. oppositifolia* were 56 °C (leaves) and 58 °C (stems), and the leaves of *S. paniculata* reached 57.5 °C (Buchner and Neuner, 2003).

Species that grow on humid sites, chionophilous rosette plants in particular, are less heat resistant: the LT_{50} for heat tolerance of *S. alpina* is 58 °C. A series of measurements on *S. pusilla* carried out by Buchner and Neuner (2003) showed a mean LT_{50} of 49.9 ± 1.6 °C and maximum LT_{50} heat tolerance of 54.6 °C. Species growing in the subnival and nival altitudinal zones are especially heat sensitive. Most psychrophytes, like *R. glacialis*, need melt water to cool the soil and keep the leaf temperatures down by transpiration cooling. Heat resistance values (LT_{50}) in leaves of *R. glacialis* ranged from 45 to 47 °C (Gauslaa, 1984; Larcher et al., 1997; Pisek et al., 1968). *In situ* measurements during midsummer showed mean LT_{50} values of 47.8 °C with a maximum of 51.3 °C (Buchner and Neuner, 2003). Other psychrophytes were also resistant to temperatures of up to 45–52 °C; for example: *Oxyria digyna*, *Geum reptans*, *Cerastium alpinum* and arctic *Saxifraga* species (Biebl, 1968; Pisek et al., 1968).

The annual course of heat resistance of vascular plants is not only synchronised with the climatic conditions but also endogenously and species-specifically determined (Kappen, 1981; Lange, 1967). There are species which show an increase in resistance during summer (S-type), species which develop increased heat resistance during winter dormancy (W-type) and finally species which hardly show any annual fluctuations in resistance at all (C-type). On the basis of their seasonal variation in heat resistance *S. acaulis*, *S. oppositifolia* and *S. alpina* belong to the W-Type. The span between peak resistance during winter and the lower level of heat resistance during summer is 3–5 K. Many herbaceous and woody plants of the temperate zones match this type (Biebl and Maier, 1969; Lange, 1961). *C. firma* shows properties of the C-type with only very small annual fluctuations of 1–2 K in heat resistance. All investigated *Sempervivum* species are distinct S-types: from winter to midsummer the heat resistance increases by 6–7 K. Under the influence of short-term hot spells or drought the span can expand to 10 K.

In the high mountains at the microclimate level air temperatures can reach values of 40–45 °C. Small-scale overheating of plant organs to up to 50–55 °C can occur. This results in a difference of 15–20 K between the heat resistance limit of most high mountain plants and the highest temperatures of the boundary layers – with no difference being measured between shoots and roots. Among the investigated species it is only *C. firma* that shows a small safety margin (10 K).

A rapid adjustment can be observed related to the high diurnal fluctuations of plant temperatures. In the case of *S. acaulis* the increase in resistance happens within hours or at least within a summer day (Buchner and Neuner, 2001). This quick protection would be established by heat-shock proteins and ubiquitine (Belknap and Garbarino, 1996; Vierling, 1991).

Multiple stresses and cross-tolerance

In open habitats in the high mountains, plants are exposed to multiple stresses and constraints, such as low temperatures, frequent freeze–thaw cycles, snow-drift and frost desiccation during winter and strong solar radiation, overheating and partial drought during summer. Due to the influences of low temperatures and frost desiccation the plants develop not only a high frost resistance but also a high desiccation tolerance (Pisek and Larcher, 1954). Likewise, any temperature stress and water shortage leads to an increase of heat resistance (Alexandrov, 1977; Kappen, 1965).

The acquisition of a cross-tolerance to climate stress during the adaptation to stress factors (Levitt, 1958) is frequently based on general stress-related gene products, which make the protoplasm generally stable (Close, 1996). Even the influence of one single stress factor like cold, desiccation, or heat and also signals for dormancy (phytohormons, like abscisic acid) may induce the synthesis of protection proteins, which provide the protoplasm with a greater resistance to various types of stress. Structural similarities of frost protection proteins (Close, 1997; Kosová et al., 2007; Sung et al., 2003; Thomashow, 1999), drought stress proteins (dehydrins and LEA proteins; Bray, 1993; Ingram and Bartels, 1996), and heat-shock proteins (Wisniewski et al., 1996), form the molecular basis for a common tolerance mechanism against climatic stress.

Frost and water deficit, as well as heat, induce an increase in the two cross-linked resistances. The individual spread of frost resistance values (Figs. 9–12) and the ecologically paradoxical increase in heat resistance during winter of *S. acaulis*, *S. oppositifolia* and *C. firma* point towards co-adaptive behaviour. The high frost resistance values of individual cushions could be caused by winter drought. Low winter values, however, are due to a constant snow cover, which at the same time protects against drought. During winter and summer random samples of several *S. acaulis* cushions were weighed and their relative water contents were calculated (RWC = (FW–DW)/(SW–DW), where FW is the fresh weight, SW is the saturated weight, and DW is the dry weight) and compared. We found a broad range of *seasonal* water saturation deficit values (WSD*seasonal* [%] = [(RWC*summer*−RWC*winter*)/RWC*summer*]*100) of 9–46% among the winter values. In early winter and under conditions of daily frosts cushions of *S. oppositifolia* show a WSD*seasonal* of 25–38%. In case of *Saxifraga caesia*, Ulmer (1937) compared the winter and summer RWC and found a WSD*seasonal* of 28–39%; in the case of *C. firma* the WSD*seasonal* was 21%. In the dwarf heath shrub heath on Mt Patscherkofel individuals of *Loiseleuria procumbens* showed varying water saturation deficits depending on the snow cover: constantly snow-covered plants remained at a stable WSD*seasonal* of 14–18% during the whole winter, snow-free plants dried out to a WSD*seasonal* of 36–45% during late winter (Larcher, 1957; Pisek et al., 1935).

Final remarks

The diversity of life-threatening climatic conditions in the high mountains has lead to the evolution of a variety of viable plant growth forms and life styles. The persistence of plant species in the rough mountain climate can either be accomplished by the ability to adapt easily to extreme temperatures (cushion plants in particular) or by escaping the temperature constraints by creating protective microsites (prostrate herbaceous plants in particular). Those plant species that stay in their habitat and show broad acclimatisation amplitudes or physiologically contrasting ecotypes (Crawford and Abbott, 1994) survive successfully. Glacial fluctuations as a result of ongoing climate change allow small-scale migration of plant species (Gottfried et al., 1998; Theurillat and Guisan, 2001; Walter and Walter, 1953). The diversity of high mountain plants with their differing survival types is crucial to their ability to cope effectively with changing climatic conditions.

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