Cornelius Lütz
Editor

Plants in Alpine Regions

Cell Physiology of Adaption and Survival Strategies

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Preface

Plants inhabiting high alpine and nival zones are considered as living in an extreme environment.

Extreme environments have been attractive for explorers for centuries, and nowadays they also attract tourists. Fortunately biological science is becoming increasingly aware that these remote habitats provide challenging questions that will help to understand the limits of life functions. Biota of cold, extreme environments have been brought closer to the scientific community and to the public by international activities such as the International Year of the Mountains (2002) or the International Polar Year (2007–2009).

While it is indispensable to use model plants such as *Chlorella, Physicomitrella, Hordeum* or *Arabidopsis* to follow single metabolic processes and pathways or fluxes, species from remote locations are difficult to use as model organisms: often they do not grow in culture or they change their metabolism completely under artificial growth.

Plants at the margins of life developed a broad range of adaptation and survival strategies during evolution. These are best studied with species growing in extreme environments – extreme firstly for the researcher, who tries to measure life functions in the field and to harvest samples for later studies in the home laboratory. This has been experienced by an increasing number of scientists working in the fields of geobotany, plant ecophysiology and ecology. Their work has prepared the conditions that allow different aspects in cell physiology of plants from cold environments (the same holds for high temperature biota e.g. of deserts, volcanoes) to be studied by state-of-the-art methods and the results to be interpreted in order to understand the entire organism, and not merely an isolated function.

This book is devoted to the presentation of a collection of articles on adaptation and survival strategies at the level of cell physiology. The plants have partially been investigated in the field and were partially taken directly from alpine or polar habitats for experiments under lab conditions.

The book contains 14 chapters, written by experts from different research areas. Most of the contributions are from scientists from the University of Innsbruck. This is not surprising since the “Alpenuniversität” looks back on more than 150 years of research in alpine regions in many fields, including biology, medicine, weather and climate, geology, geography and others. Surrounded by high mountains, the university still is a center of alpine research today. Several topics have been taken up by colleagues from other universities to integrate their challenging work for a better description of alpine plant cell physiology.

If physiology and cell structural research are not to lose the connection to the organism, at least partial knowledge of the environmental conditions as determinants of most life functions should be considered. Therefore, the first three chapters deal with aspects of the physical environment of alpine plants.

In Chap. 1, *M. Kuhn* explains the conditions of water input in the form of snow or rain in the High Alps. Seasonal variations, regional differences and altitudinal effects or wind exposure strongly determine water and snow situations for the plant communities. The physical characterization of snow cover will help to understand plant survival in winter. Equally important for plant life and development is solar radiation, characterized by *M. Blumthaler* in Chap. 2 for the European Alps. Radiation physics is not an easy issue for plant scientists, but it is well explained in this context. The variation in solar radiation input in the Alps comes from atmospheric factors such as aerosols, dust, clouds, ozone, and further depends on altitude, solar angle and exposure angle of a plant surface to the sun. The biologically effective UV radiation is at the center of this contribution. Chapter 3 by *W. Larcher* deals with the bioclimatic temperatures of mountain plants and connects the first two chapters with the microclimate which is closer to the plants than general weather descriptions allow. Macro- and microclimate temperatures show large differences. Less often taken into account, but of enormous influence are soil temperatures in mountain regions. Soils buffer the large diurnal temperature changes in high altitudes, thus influencing root growth. Recording actual temperatures at the plant body or in the canopy provides important data for understanding plant growth forms and the physiology of temperature adaptation.

The following Chap. 4 by *C. Lütz* and *H.K. Seidlitz* describes effects of anthropogenic increases in UV radiation and tropospheric ozone. Sophisticated climate simulations demonstrate that alpine vegetation as well as one of the two Antarctic higher plants will probably not suffer as a result of the expected increases in UV. In contrast, ozone, which accumulates at higher levels in European mountains than in urban environments, may threaten alpine vegetation by inducing earlier senescence. In a combination of physiological and ultrastructural studies, *Lütz* et al. (Chap. 5) describe cellular adaptations in alpine and polar plants. Chloroplasts show structural adaptations, only rarely found in plants from temperate regions that allow them to use the short vegetation period in a better way. Possible control by the cytoskeleton is discussed. These observations reflect high photosynthetic activities; and development of membranes under snow in some species is documented. By contrast, the dynamic of high temperature resistance in alpine plant species is presented by *G. Neuner* and *O. Buchner* (Chap. 6). Tissue heat tolerance of a large number of alpine species is reported. Heat hardening and developmental aspects are compared. As high temperatures in the Alps normally occur under high irradiation, the authors look more closely at the thermotolerance of photosystem II. Acclimation of photosynthesis and related physiological processes in a broader view are discussed by *P. Streb* and *G. Cornic* in Chap. 7. Aspects of acclimation in alpine plant photosynthesis include C4 and CAM mechanisms and the PTOX electron shuttle. The protection of photosynthesis by energy dissipation and antioxidants is also considered.

R. Bligny and *S. Aubert* (Chap. 8) investigate metabolites and describe high amounts of ascorbic acid in some Primulaceae. By using sophisticated NMR methods they also identify methylglucopyranoside in *Geum montanum* leaves, which may play a part in methanol detoxification, and finally study metabolites in *Xanthoria* lichens during desiccation and hydration. In Chap. 9 *F. Baptist* and *I. Aranjuelo* describe metabolisms of N and C in alpine plants – often overlooked by physiologists. Plant development depends greatly on carbon fixation and a balanced N uptake by the roots. Snow cover and time of snow melt determine N uptake for the metabolism. Storage of C and N in alpine plants under the expected climate changes is described and discussed.

The high mountain flora shows that flowering and seed formation function despite the often harsh environmental conditions. In Chap. 10 *J. Wagner* et al. explain how flower formation and anthesis are regulated by species-specific timing based on the plant organ temperatures. Snow melt – again – and day length control reproductive development and seed maturity.

The next two chapters report on recent findings describing adaptation to subzero temperatures. As *S. Mayr* et al. show (Chap. 11), alpine conifers are endangered in winter by limited access to soil water, ice blockages of stored water in several organs, and frost drought in the needles. Embolism and refilling of xylem vessels are studied by biophysical methods and microscopy, resulting in a better understanding of the complex hydraulics in wooden alpine plants. Thematically related, *G. Neuner and J. Hacker* discuss freezing stress and mechanisms of ice propagation in plant tissues (Chap. 12), using alpine dwarf shrubs and herbs. Resistance to freezing stress depends greatly on plant life forms and developmental stages. The capacity of supercooling is studied in some species. By means of digital imaging they describe ice propagation in leaves and discuss the structural and thermal barriers in tissues that are developed to avoid ice propagation.

D. Remias continues with snow and ice (Chap. 13), now as a habitat, and reports on recent findings in the cell physiology of snow and ice algae from the Alps and polar regions. The extreme growth conditions require special metabolic and cell structural adaptations, such as accumulation of secondary carotenoids ("red snow") in the cytoplasm, or vacuolar polyphenols as a protection against high PAR and UV radiation (glacier ice algae). Photosynthesis is not inhibited by zero temperatures and not photoinhibited under high irradiation – comparable to many high alpine species. Even smaller in size, but best acclimated to cold temperatures are microorganisms in alpine soils, presented by *R. Margesin* in Chap. 14. These organisms serve as ideal study objects to characterize cold active enzymes, cold shock proteins and cryoprotectans. Microbial activity in alpine soils at low temperatures has an important influence on litter decomposition and nutrition availability, which connects to higher plant root activities.

After many years of studying alpine and polar plants under different aspects, it was a pleasure for me to edit this collection of research contributions; I thank all colleagues for their participation and effort in presenting their data.

I hope that this book expands the information on cell physiology of alpine/polar plants including the connection to the physical environment they are exposed to. The different contributions should encourage more scientists to incorporate plants from extreme environments in their studies in order to understand the limits of cellular adaptation and survival strategies.

Finally I would like to thank the Springer team for their support and valuable suggestions on editing this book, especially Dr. A.D. Strehl and Mag. E.M. Oberhauser.

Innsbruck, spring 2011 Cornelius Lütz

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Rain and Snow at High Elevation

The Interaction of Water, Energy and Trace Substances

1

Michael Kuhn

1.1 Introduction

Plants are major players in the alpine biogeochemical cycles, using water, energy and nutrients from both the atmosphere and the ground for their primary production. They are exposed to rain and snowfall, may be covered by snow for considerable periods, absorb solar radiation and transpire water vapour back to the atmosphere. While the supply of energy, water and nutrients from the atmosphere is the boundary condition for the plants' existence, they significantly determine the return of all three quantities back to the air.

Bioclimatic temperatures in the high Alps are treated in the chapter by Larcher, the supply of solar radiation by Blumthaler. This chapter deals with the significance of rain and snow for high alpine plants. It describes the regional and local distribution of precipitation, its change with elevation and its seasonal course. It emphasizes the importance of snow as a place of water storage, thermal insulation and concentrated release of ions.

1.2 Regional, Vertical and Seasonal Distribution of Precipitation

1.2.1 Annual Precipitation

The regional distribution of annual precipitation in the Alps has been analysed repeatedly, I recommend reading Fliri (1975), Baumgartner and Reichel (1983), Frei and Schär (1998) and Efthymiadis et al. (2006) for that purpose. All of these authors agree that the distribution of alpine precipitation is dominated by two independent variables: altitude and windward situation (or distance from the northern and southern margins toward the interior Alps).

In the Eastern Alps, the majority of annual precipitation arrives either from the SW or NW, with the passage of a trough on its eastward way from the Atlantic. This explains the frequent succession of south-westerly flow with precipitation at the southern alpine chains followed by north-westerly currents wetting the northern part of the Eastern Alps, a pattern that was described by Nickus et al. (1998): "A trough moving in the Westerlies and moving near the Alps will cause a south-westerly to southerly flow over the Eastern Alps. Precipitation south of the central ridge and Föhn winds in the north are the most frequent weather situation at this stage. With increasing cyclonality air flow will become more westerly, often bringing moist air from the Atlantic. Precipitation will then shift to the central and northern parts of the Alps, starting in the west and continuing to the east. As the flow turns to more northerly directions, a passing cold front may bring precipitation mainly in the northern parts of the Alps and at least an interruption in precipitation in the south."

A consequent rule of thumb is that stations at the northern and southern margins experience three times as much annual precipitation as those in the dry interior valleys (Fliri 1975), in rough figures 1,500–500 mm, with maxima at some stations exceeding 3,000 mm and minima of less than 500 mm per year. In either case, the highest of the central chains experience a secondary maximum as the Glockner Group in Fig. 1.1 (at 47°N and 12.5–13.5°E).

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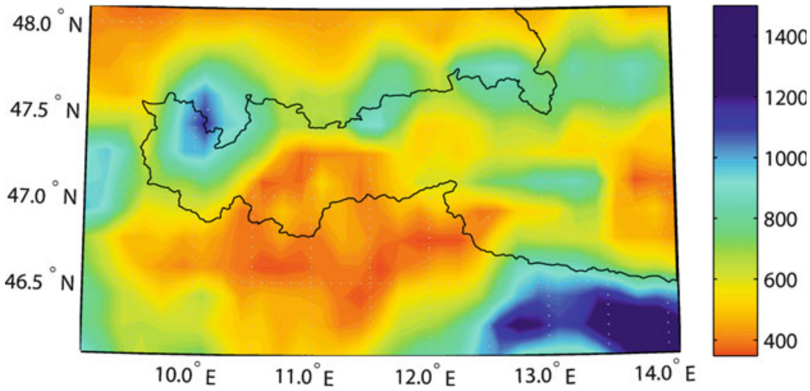

Fig. 1.1 Winter precipitation (December, January, February) in the Eastern Alps according to the HISTALP analysis, in mm. The HISTALP precipitation data set is described by Eftymiadis et al. (2006)

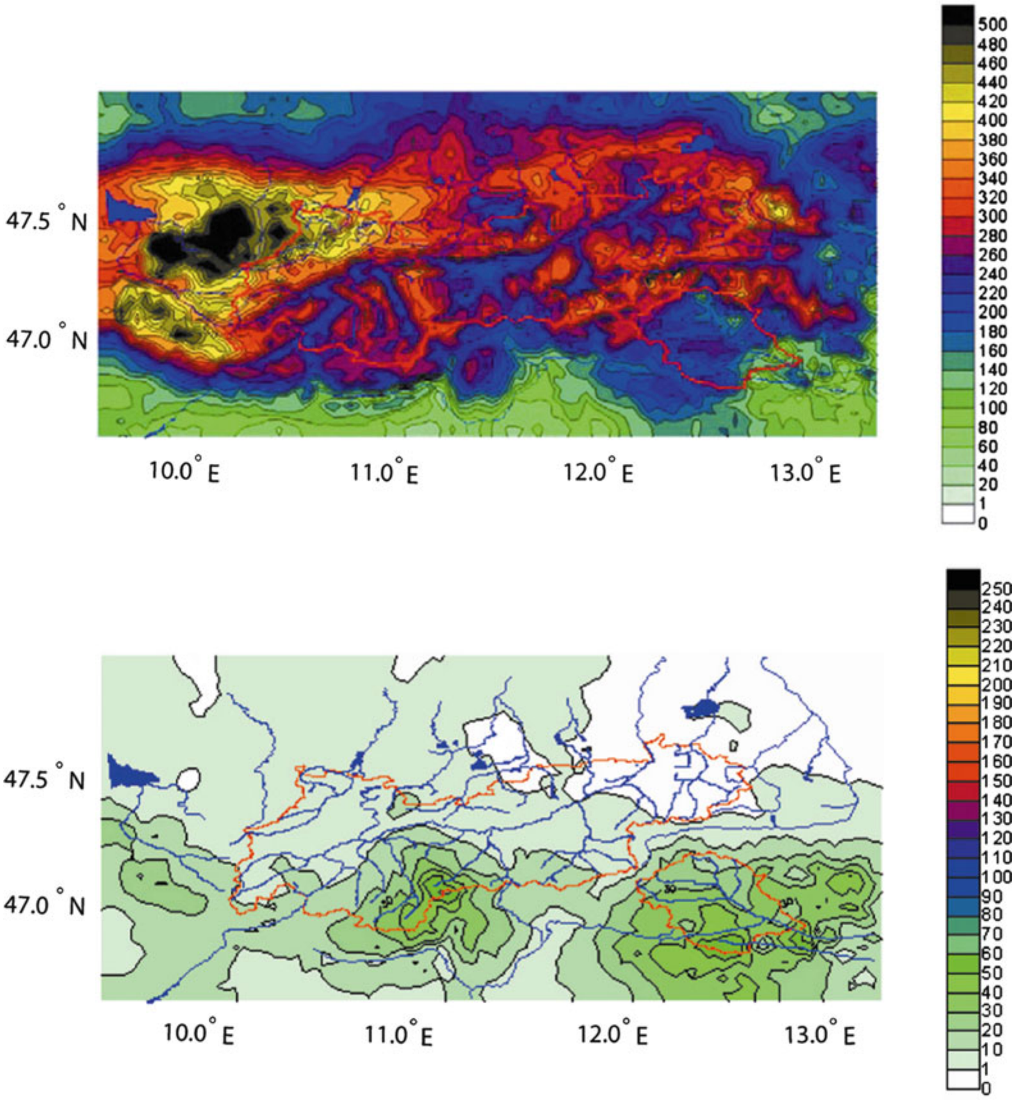

Fig. 1.2 Total precipitation of the month of August 2010 (*above*) is dominated by north-westerly flow with values exceeding 400 mm in the west and less than 200 in the south-east. The daily sums from 14-08-2010, 07:00 to 15-08-2010, 07:00 given in the *lower* panel describe a situation of southerly flow. From Gattermayr (2010)

The annual values given above are the sums of many individual events. Two examples of these are given in Fig. 1.2. Be aware, however, that many of the details on these precipitation maps are interpolated with algorithms that use elevation and distance from actual meteorological observations as independent variables.

1.2.2 Effects of Elevation

Several effects contribute to the higher incidence of precipitation at higher elevations: temperature is lower at higher elevation, the water vapour is thus closer to saturation, and condensation is more likely at higher elevation; when moist air is advected towards a mountain chain, it is forced to ascend and thereby cools; wind speed, and thus horizontal advection of moisture, increases with elevation, the decisive quantity being the product of horizontal wind speed and water vapour density.

Altogether an increase of about 5% per 100 m elevation is observed in various valleys of the Eastern Alps as shown in Fig. 1.3. The annual course of the increase of precipitation with elevation shown in Fig. 1.3 reflects the varying frequencies of advective and convective precipitation. In winter and spring the advective type, associated with the passage of fronts, dominates and leads to high values of the vertical gradient of precipitation. In summer convective precipitation prevails; it depends on local heat sources which are by and large independent of elevation. Convective precipitation most likely occurs over sunlit slopes with vegetation. As both energy supply and vegetation decrease with elevation, convective precipitation may even have an upper limit and thus a lesser increase with elevation; it is certainly more influenced by exposition than by elevation and decreases the mean monthly values of vertical gradients of precipitation given in Fig. 1.3.

1.2.3 Seasonal Variation of Precipitation

The seasonal course of precipitation in the Eastern Alps (e.g. 10°E) has a marked change with latitude. In the north, there is a clear dominance of summer rainfalls, monthly sums may be three times as high as those of fall and winter. A summary presentation by Fliri (1975, his Figs. 69–75) shows this summer maximum to extend southward into the dry, central region. Farther south the Mediterranean dry summers split the precipitation curve into two maxima in spring and fall,

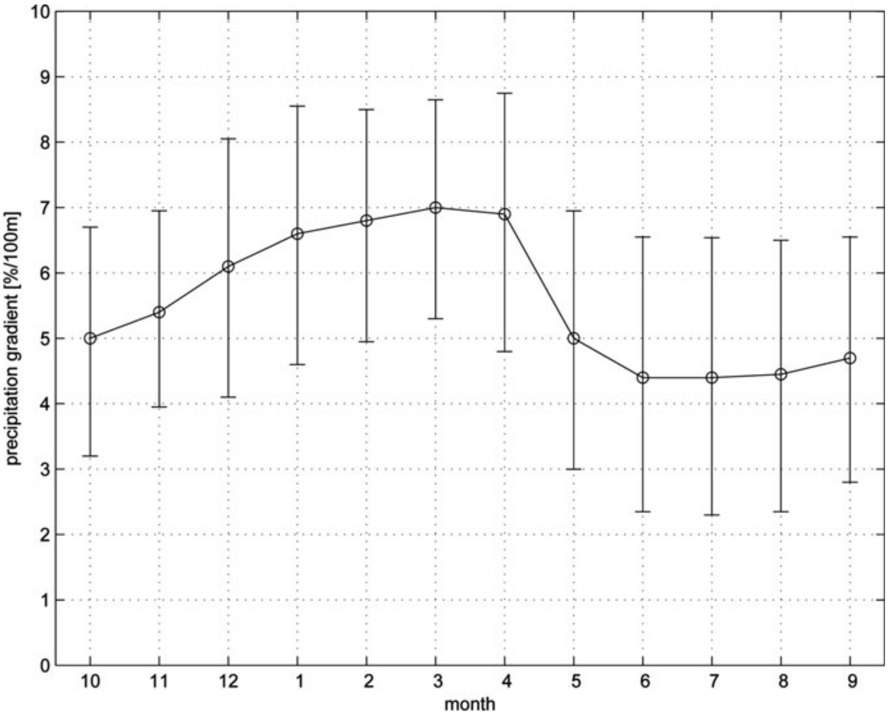

Fig. 1.3 The increase of annual precipitation with elevation, expressed as % per 100 m elevation. Bars indicate upper and lower limits of 10 hydrological basins (Kuhn 2010)

the latter often dominating. This is locally diverse, but generally evident in Fig. 1.4.

An analysis of recent years has shown that the climatological means in Fig. 1.4 have a high interannual variance and that deviations from the mean have a tendency to come in groups of several years. This is true in particular for the occurrence of October and November maxima.

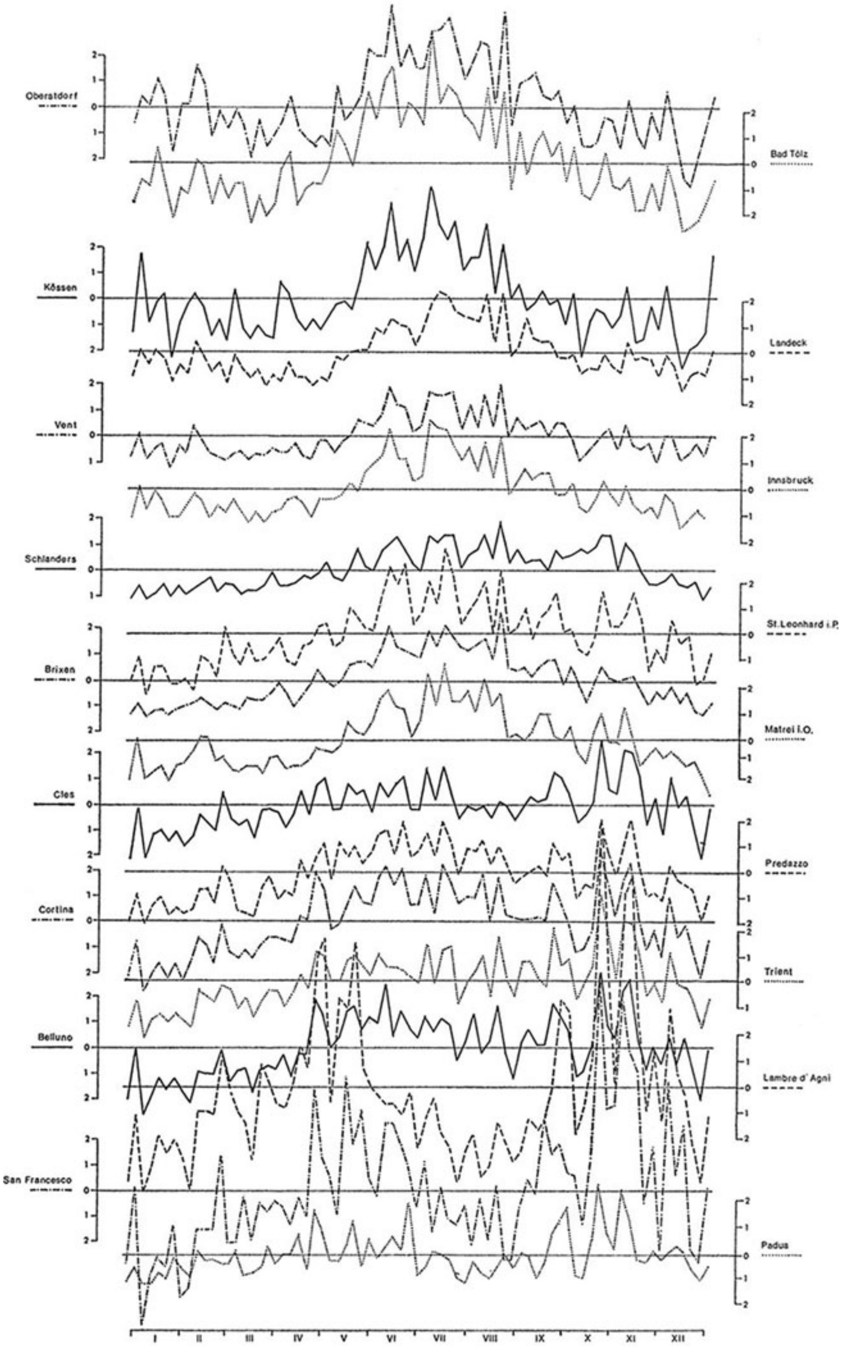

Fig. 1.4 Annual course of monthly precipitation in a cross section from N to S, approximately 10–12°E, in mm per day. Means of 1931–1960, from Fliri (1975)

1.3 Snow Cover

1.3.1 The Transition from Rain to Snow

The transition from snow to rain is expected to depend on the 0°C limit. Even at the level of formation of snow flakes it is not exactly the air temperature that determines the freezing of precipitation; it is rather the energy balance of the drop or flake, best approximated by the so called wet bulb temperature which is determined by evaporation and sublimation: at a given air temperature, drops would rather turn into snow flakes at low relative humidity. Snow forms at higher and therefore colder levels so that surface temperatures of about 1°C are an alpine-wide useful approximation for snowfall. The probability of snowfall Q may be expressed by $Q = 0.6–0.1\ T$.

The fraction of solid vs. total precipitation depends on elevation as shown in Fig. 1.5. Considering the fairly regular dependence of temperature on elevation in this figure, it is remarkable that the fraction of solid vs. total precipitation has a much higher variance than that of temperature. The absolute values of solid precipitation F and those of total annual precipitation are dominated by their regional distribution more than by altitude.

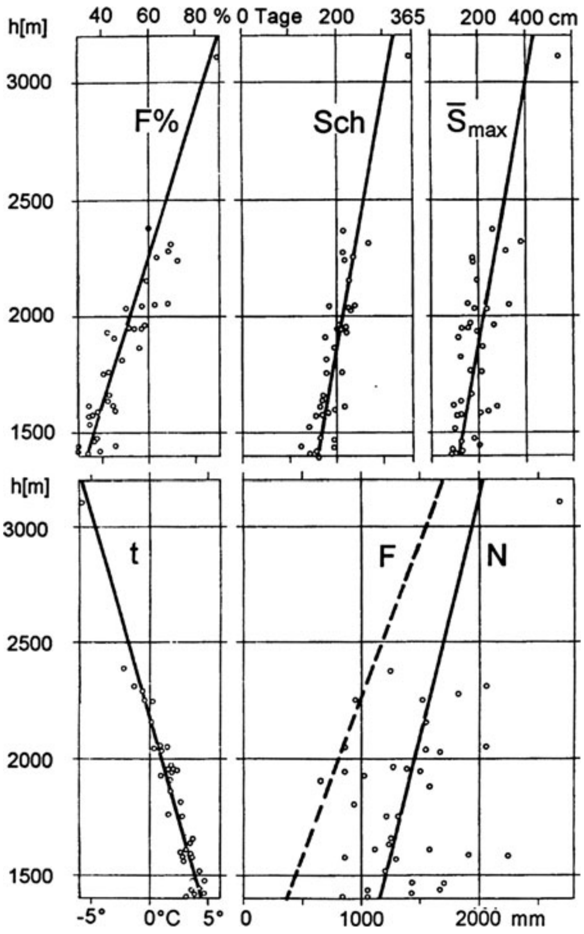

Fig. 1.5 Dependence on elevation of various quantities describing snow cover: F% fraction of solid vs. total precipitation; Sch duration of the snow cover in days; $\overline{S}_{max}$ annual means of maximum snow height; t temperature in °C; absolute values of solid F and total annual precipitation N in mm (Kuhn 1994 according to data by Lauscher)

1.3.2 Accumulation vs. Snowfall

There are several indicators of the amount of snow on the ground. Snowfall per se is best expressed as water equivalent, i.e. the height of its melt water, in mm (or kg per m^2). Fresh snow typically has a density of 100 kg m^{-3} which means that a snow cover of 10 cm has a water equivalent of about 10 mm. With a typical mean density of the winter snow cover of 300–400 kg m^{-3}, snow packs of 3 m height may be expected at elevations above the tree line; snow packs of 6 m have occasionally been observed in the Austrian Alps.

Once the snow has fallen it is generally redistributed by wind drift, also by avalanches. The amount finally lying on the ground is called accumulation and is expressed in terms of water equivalent. Wind takes snow away from ridges and crests and deposits it in concave terrain where the total accumulation may be twice as high as the original snow fall.

On a small scale, the redistribution of snow may create long lasting covers that profoundly influence vegetation. There are cornices on crests that survive into summer, and creeks that collect and preserve snow (called Schneetälchen in German literature), and there are, on the other hand, crests that are blown free of snow and may suffer much lower soil temperatures than their snow covered, insulated surroundings.

The duration of snow cover at a given elevation has been averaged for all Austrian stations and compared to the mean winter temperature at these stations. With the proper choice of scales, the two curves match very closely in Fig. 1.6.

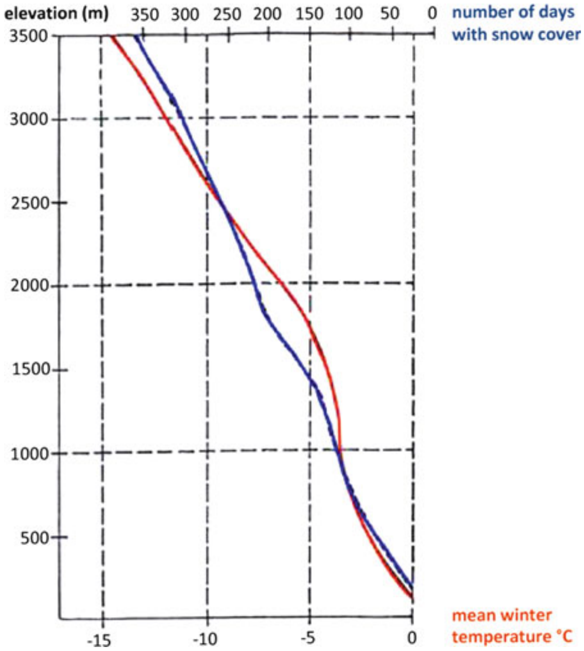

Fig. 1.6 Duration of snow cover in days and mean winter temperature vs. elevation, from Austrian stations

The seasonal development of the snow cover is determined by both accumulation and ablation. The two graphs in Fig. 1.7 show modelled snow water equivalent vs. elevation in monthly profiles from October to September for the relatively dry basin of the Rofen Valley and for the relatively humid Verwall Valley. In May at 3,050 m elevation, the snow cover in Rofen Valley is about 700 mm w.e., that in Verwall Valley is 1,400 mm w.e. From October through March both valleys have snow covers with low vertical gradients. These are determined mostly by accumulation which in turn increases above the rain/snow limit (compare the fraction of solid precipitation in Fig. 1.5), and in each month these gradients increase with elevation. In April and May, ablation starts at low elevation and diminishes the snow water equivalent, while accumulation keeps adding to the snow cover at high elevation. Thus, strong vertical gradients of snow water equivalent appear in both regions.

These two examples are mean basin values, to which local deviations to either side are caused by exposure and topography. They do, however, clearly show the natural differences in snow line elevation that exist between the dry central regions and the wet margins: Rofen Valley 3,150 m, Verwall Valley 2,550 m. In May the snowline in the early vegetation period is at 2,350 m elevation in Rofen Valley, while it is at only 1,950 m in Verwall Valley during the same period.

1.3.3 Energy and Mass Balance of the Snow Pack

The development of the snow pack is influenced by surface temperature, and hence by air temperature in two ways: temperature determines the transition from rain to snowfall; and it determines surface melting and sublimation via the energy balance of the snow (e.g. Kuhn 2008).

In the Eastern Alps, melting is the predominant form of snow ablation, it consumes an amount of 0.33 MJ kg^{-1}, subsequent evaporation requires 2.5 MJ kg^{-1}. The energy balance of a melting snow cover is

$$S\downarrow + S\uparrow + L\downarrow + L\uparrow + H + C + LS + LM = 0$$

where S is incoming and reflected solar radiation, L long wave (infrared) radiation, H turbulent sensible heat transfer, C is heat conduction in the snow, LS heat required for sublimation and LM for melting. LS includes all water that is first melted and then evaporated while LM represents the melt water that actually runs off. The fluxes S↓ and LM are not restricted to the surface but may turn over energy within the snow cover. This is due to solar radiation penetrating into the snow pack and due to melt water percolating and delivering heat to the colder interior.

Snow is a very efficient thermal insulator, which implies that strong vertical temperature gradients may exist in the snow pack. In Fig. 1.8 snow in contact with the soil remains close to 0°C all winter, while a thin top layer may cool down to about –20°C. Associated with these temperature gradients there are gradients of vapour pressure in the snow pack (saturation vapour pressure decreases by a factor of about 2 for each decrease in temperature by 10°C) which in turn lead to a transport of water vapour by diffusion in the pore space, sublimating mass from the lowest snow layers and depositing it above as so called depth hoar. This effectively changes the structure and stability of the lowest snow layers, enabling gas exchange between soil and snow.

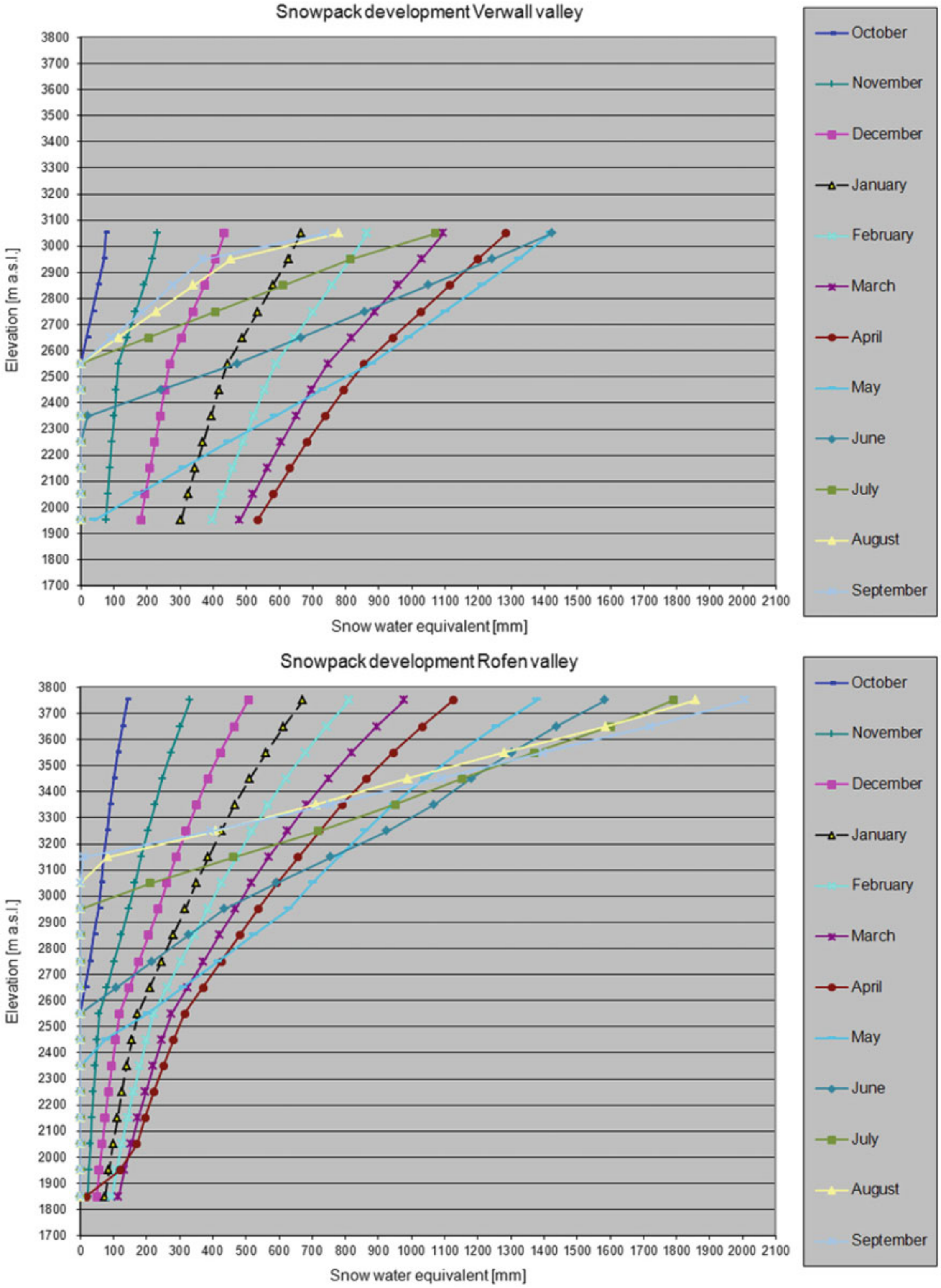

Fig. 1.7 The seasonal development of the snow cover vs. elevation modelled for two basins. Values are given in mm water equivalent. *Top*: the basin of Verwall (47.1°N, 10.2°E) with abundant precipitation, bottom: the relatively dry basin of Rofen (46.8°N, 10.8°E). Compare the peak values of snow cover at 3,000 m, and the snow line elevation in September

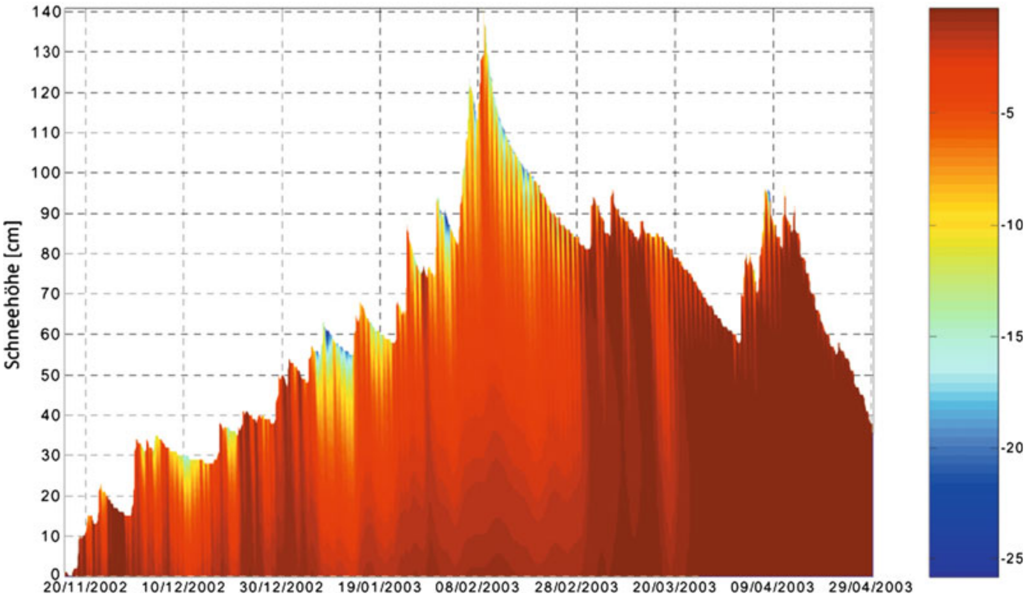

Fig. 1.8 The distribution of temperature in the snow pack at about 2,000 m elevation in the central Alps. Note the downward penetration of the daily temperature cycle and the associated phase lag. The scale on the right is in °C. From Leichtfried (2005)

1.3.4 Percolation of Rain and Melt Water Through the Snow Pack

With occasional rains in winter and with the daily melt cycle in spring, liquid water penetrates into the snow, where it soon refreezes during the accumulation period, forming ice lenses or horizontal layers that may impede vertical gas diffusion. In spring the melt water front will progressively penetrate deeper and will finally reach the soil within a few days. The percolation of melt water was modelled in Fig. 1.9 which is identical to the snow pack in Fig. 1.8.

1.3.5 Microscale Contrasts in a Broken Snow Cover

At elevations of 2,000–3,000 m global solar radiation may reach peak values of 500 W m^{-2} in early spring and 1,000 Wm^{-2} in June. This is usually more than sufficient to melt the snow which then has a surface temperature of 0°C. Dark, low albedo objects protruding from the snow, like rocks, trees or patches of bare ground, may then absorb so much solar radiation that in spite of their cold surroundings they may reach exceptionally high temperatures at a small local scale.

An example is given in Fig. 1.10 which displays the record of surface temperature of a rock of 2 m diameter extending half a meter above the snow. With a low albedo of 20% (compared to 70% of the snow), and lacking any energy loss by evaporation, it reached a surface temperature in excess of 37°C in the afternoon. Similar values have been observed on the lower parts of trees. In both examples heat is stored into the night and is transferred to the surrounding snow, soon creating bare patches around the trees or the rocks.

1.4 Acid Deposition at High Altitude

Aerosol particles and ions reach the alpine regions by dry deposition, such as dust from local sources or from long distances like the Saharan desert, or by wet deposition in rain and snow. Even if the source strength at far away places remained constant, the deposition in the Alps would always be controlled by both advection and convection, i.e. by synoptic conditions and by local atmospheric stability.

For the Alps, sources of air pollution are in the NW and in the industrial areas of northern Italy. In the typical series of synoptic events that was described in Sect. 1.2.1, it is the Eastern Alps that receive more wet deposition than the Western end of the Alps (Nickus et al. 1998).

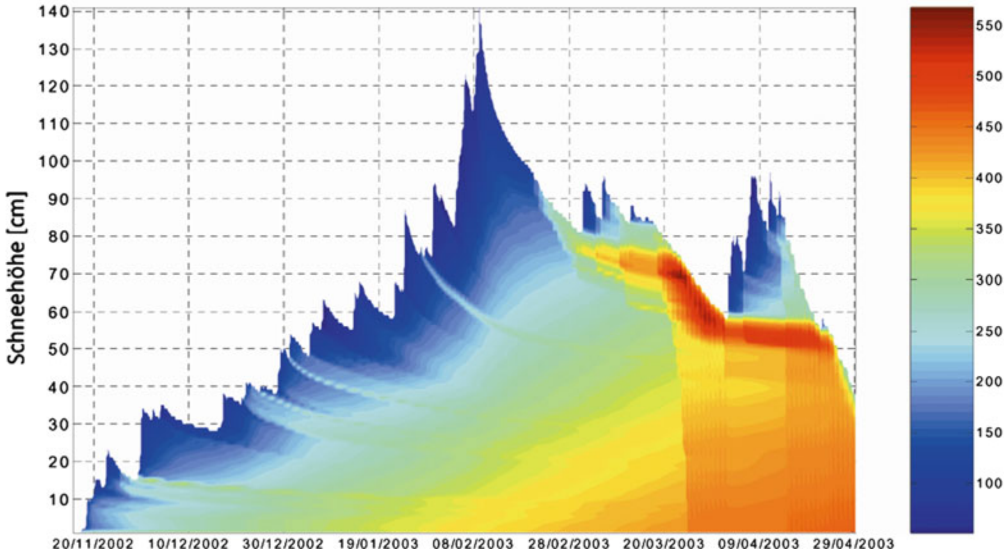

Fig. 1.9 Liquid water content of the snow pack, given as parts per thousand of the pore space on the right-hand scale. The site is identical to that in Fig. 1.8. From Leichtfried (2005)

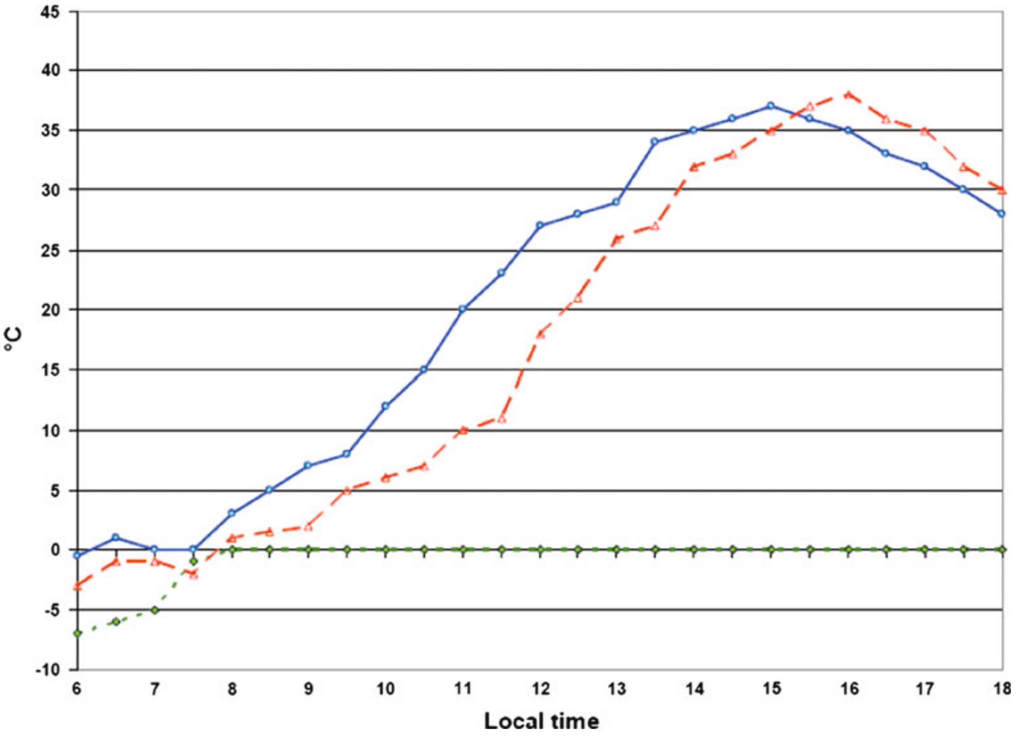

Fig. 1.10 Records of surface temperature of a rock of 2 m diameter, 0.5 m height, surrounded by snow on a clear summer day at 3,030 m. *Green curve*: snow temperature, blue south face of the rock, red west face

The seasonal development of ion concentration (μequivalents per L) and of total deposition (μequivalents per m^2) in the high alpine snow pack is generally characterized by low values in winter due to both low source strength with large areas of Europe being snow-covered, and strong atmospheric stability