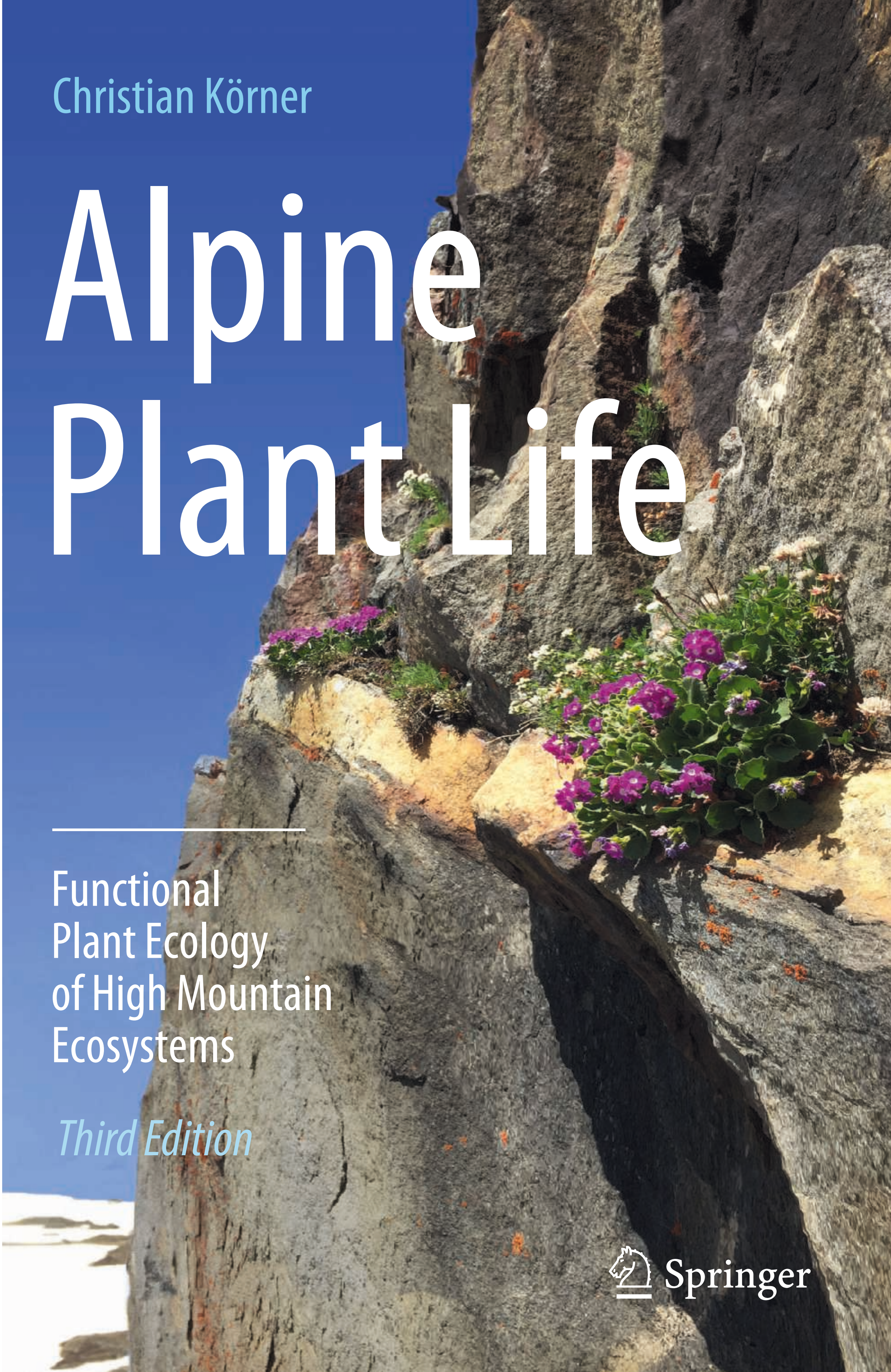
Christian Körner

Alpine Plant Life

Functional Plant Ecology of High Mountain Ecosystems

Third Edition



Springer

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Third Edition

With 327 Figures and 49 Tables

Springer

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Cover illustration: The challenges of living in a high elevation world. Alpine *Primula hirsuta* on a cliff near Furkapass, Swiss Alps.

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Preface to the third edition

Between writing the first edition 1996–1999 (a brief update in 2003) and the works on this third edition (2018–2020) more than 20 years elapsed, with the literature in alpine plant ecology presumably doubled or tripled. In this third edition, all chapters had to be refurnished for e-book customers, with the list of the substantially extended scientific literature moved to the individual chapters. All chapters had been completely re-worked, with Chaps. 1, 5, 6, 10, 16, and 17 having gone through the most substantial changes and extensions. The possibility to add color and photographs added to the visual attractiveness of this new edition.

For this book not to become an exhaustive review but retaining a readable format, I had to be selective with what to present, but I do realize, that at places I was carried away in an attempt at reflecting as much evidence as possible. So I ask readers to acknowledge the dilemma, between the flood of new information on the one hand, and the need to arrive at a readable text on the other hand. In a longer-term writing project such as this one, new references keep coming in for completed chapters as one progresses from one topic to the next. It was difficult to keep updating across all chapters, although I maintained feeding my (1972 initiated) personal literature database (23’000 entries including the c. 4’000 references for this volume), with many (older) sources that would not show up in the web of science. Without this very efficient literature database, I could not have achieved this task. I thank Jens Paulsen for customizing and maintaining it, and generations of student helpers who were entering my comments from notes on reprints, in order to complete and extend the often marginally useful information in abstracts.

As with the earlier two editions, all artwork was refurnished and/or newly produced by Susanna Riedl. The appearance of this volume carries Susanna’s fingerprint and reflects her sense for colors and proportions. I am particularly grateful to Erika Hiltbrunner for her motivation to engage myself in this re-edition project and reading and critically commenting on various chapters. I also thank Johanna Wagner (Chap. 16), Fred Meins (Chap. 14), and Thomas Fabbro (Chap 16), for editing specific sections. A large number of people helped with references or unpublished data, photographs, site and species information, field site access, fruitful discussions or support during the two-and-a-half-year process of re-shaping and updating this book: R. Albert, M. Arroyo, S. Bader, E. Barmettler, S. Beck, J. Birks, T. Buser, L. Cavieres, A. Erhardt, A. Fajardo, M. Grube, A. Hemp, J. Kadereit, Kaiser,

G. Kaser, G.M. Klug, R. & R. Körner, A. Mark, E. Meyer, P. Möhl, S. Nagelmüller, G. Neuner, C. Newesely, F. Oehl, R. G. Patthey, L. Patty, H. Pauli, F. Piper, R. Psenner, B. Sattler, E. Spehn, J. Stöcklin, H. Sun, U. Tappeiner, Y. Willy, Y. Yang. I am grateful to all of them. I also thank Zuzana Bernhart, Albert Paap, Saranya Kalidoss and Ritu Chandwani at Springer for their efforts towards publishing the book.

Over the past years, I became sensitive to the importance of a well-defined terminology. In this new edition, I cared for refining vocabulary. Classics are, for instance, the meaning of what is 'alpine', what is a 'treeline' (and what not), a tundra, stress and limitation, which climate is relevant and which is not. For the alpine world to have a clear delineation, the climatic treeline had to be defined more precisely (Chap. 7), while at the same time permitting to quantify global alpine land area by geographical information systems. With the alpine biome spanning across all terrestrial latitudes, the Arctic tundra is its northern, low elevation tail. So there is no such thing as an 'alpine tundra', because the tundra is, by definition, a specific part of the treeless Arctic.

A lot of the novel research presented in this edition originated from the Furka Pass region of the Swiss Alps. This underlines the immense significance of a well equipped field station that provides immediate access to nature, in this case, a hotspot of alpine biodiversity that serves monitoring low– and high–tech experimental research (Fig. 1.16), as well as teaching alpine plant ecology.

The Swiss Alpine Research and Education Station, ALPFOR, at Furka pass, 2430 m, with the 3586 m Galenstock in the back, greatly contributed to the contents of this book (photo by E. Hiltbrunner). See www.alpfor.ch

In the course of this attempt at improving and updating the earlier editions, this almost became a new book. I hope that this new Alpine Plant Life will help experienced readers to access topics of interest rapidly and instructively, and guide newcomers to this fascinating field of research, getting started on solid ground. Finally, I hope this colorful edition will assist many in teaching and learning about alpine plant ecology.

Basel
September 2020

Christian Körner

Preface to the second edition

Recent years have seen renewed interest in the fragile alpine biota. The International Year of Mountains in 2002, and numerous international programs and initiatives have contributed to this. Since nearly half of mankind depends on water supplies originating in mountain catchments, the integrity and functional significance of the upland biota is a key to human welfare and will receive even more attention as water becomes an increasingly limited resource. Intact alpine vegetation, as the safeguard of the water towers of the world, is worth being well understood. This new edition of *Alpine Plant Life* is an update with over 100 new references, new diagrams, revised and extended chapters (particularly 7, 10, 11, 12, 16, 17) and now also offers a geographic index. My thanks go to the many careful readers of the first edition for their most valuable comments, in particular to Vicente I. Deltoro (Valencia) and Johanna Wagner (Innsbruck).

Basel — Christian Körner
April 2003

Preface to the first edition

One of the largest natural biological experiments, perhaps the only one replicated across all latitudes and all climatic regions, is uplift of the landscape and exposure of organisms to dramatic climatic gradients over a very short distance, otherwise only seen over thousands of kilometers of poleward traveling. Generations of plant scientists have been fascinated by these natural test areas, and have explored plant and ecosystem responses to alpine life conditions. *Alpine Plant Life* is an attempt at a synthesis.

This book has roots in a century of research into alpine ecology at the Institute of Botany in Innsbruck, Austria. Anton Kerner pioneered the field in the late nineteenth century. Arthur Pisek founded modern comparative and experimental ecology of alpine plants and was the first to systematically combine field with controlled environment studies. Walter Larcher introduced the ecosystem approach, the question of scale. During my doctoral project with him on alpine plant water relations, he stimulated my interest in links between plant structure and function and in plant developmental processes. My former senior colleague Alexander Cernusca introduced me to environmental physics and thanks to him I began to think in terms of fluxes and pools. This text could not have been written without these influences.

Privileged to grow up in a green environment, my interest in biology was stimulated by my parent's fascination in plants and landscape gardening, their painting and photography, and their strong feel for natural aesthetics. Alpine vegetation is often like a garden, a mosaic of beauty, a small-scale multitude of ways of coping with life, attractive to both the naturalist and the scientist. Perhaps the reader will also find some morsels of this fascination between the lines of this scientific text.

Essential contributions to this volume were the patience and help by my wife Raingard and the graphical work, help with literature and laboratory analysis by Susanna Pelaez-Riedl. I am grateful to J. Arnone, E. Beck, M. M. Caldwell, T. Callaghan, F. S. Chapin, M. Diemer, B. Holmgren, S. Pelaez-Riedl, F. Schweingruber, J. Stöcklin, and H. Veit for commenting on drafts of various parts of the text. A number of colleagues helped with information, plant samples or unpublished data, namely W. D. Bowman, J. Gonzalez, S. Halloy, W. Larcher, G. Miehe, J. Paulsen, H. Reisigl, R. Siegwolf, M. Sonesson, R. C. Sundriyal, U. Tappeiner, and P. Volko. R. Guggenheim and his team produced the scanning electron micrographs in Chaps. 9 and 16. H. Schneider assisted with the electronic treatment of photographs. The University of Basel provided an ideal environment for

research and teaching alpine ecology to students and permitted the needed work-leave. I thank the Abisko Research Station, in N-Sweden, for hosting me during much of the literature and text work.

I gratefully acknowledge the fruitful cooperation with the Springer team throughout this project. In particular, I would like to thank Zuzana Bernhart, Saranya Kalidoss and Ritu Chandwani.

Alpine Plant Life was written for a broad readership. This has made it necessary to start several chapters with rather general introductions. On the other hand, I have tried to cover the bulk of scientific findings. In trying to cover as many relevant topics as possible, the reader will often only be given a reference to find answers elsewhere. There is no way to treat this field of science exhaustively in a single volume like this. Hence, the product is a compromise, which hopefully will interest the specialist, as well as a wider audience.

Basel　　　　　　　　　　　　　　　　　　　　Christian Körner
February 1999

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About the author

Christian Körner was born in 1949 in Austria, received his academic education at the University of Innsbruck, and was a full professor of Botany at the University of Basel from 1989 to 2014. As Emeritus Professor, he is continuing alpine plant research in the Swiss Alps.

Epilogue

Species occur at locations at which their traits match the local challenges so that they can persist. While it is of great interest to find out how the local populations of species manage to cope with their environmental demands, this sort of research—as summarized in this book—will in large lead to the respectful insight 'how well species cope'. The ones that do not cope are missing. Hence, from such data we do not learn why a species is confined to certain microhabitats, and species range limits remain largely unexplained. Some hypotheses may be formulated though, based on the local life conditions and responses. In other words, the most fundamental question of wildlife, including plant ecology, why organisms occur where they do, remained largely unanswered (Körner et al. 2016).

In the alpine world it is particularly difficult to identify range limits at landscape scale, because species distribution follows habitat mosaics at meter or even centimeter scale. Low temperature driven range limits may depend on a suite of structural, metabolic or developmental adaptations, each of which alone or in combination with other traits may set the limit. In order to explore the range controlling mechanisms, we need to know where the range limits are and what exactly the life conditions are at that local limit. These are local range limits, replicated many times across micro-habitat mosaics in a given mountain terrain. As was explained in Chap. 4, and touched upon in several other chapters, plants nest in and create specific microclimates. So, by their very presence, they influence their life conditions, provided they got there and established. By exploring these patterns of occurrences combined with life conditions, one can approximate the habitat conditions which define the edge of the fundamental niche, the only type of boundary that permits attributing a physiological explanation.

Once the 'where-question' had been resolved, the 'why-and-how-questions' can be explored at the edge of the species range, with this book hopefully providing some guidance towards likely and less likely traits and processes. As I tried to explain in various chapters, the more likely range-setting traits are developmental ones (timing issues, tissue formation) or stress-physiological ones (freezing tolerance, early seedling stage survival). Neither carbon nor nutrient relations hold any promise to explain species range limits, and thus, species distribution, although both these traditional fields of alpine ecology are important for explaining the day-by-day plant functioning, the vigor and the abundance of established plants in a competitive community.

In a nut shell, this book explains that alpine plants grow and develop in such a way that they create and capitalize on a warm microclimate with appropriate morphology (stature) and timing of development (phenology). The outcome are carbon and nutrient relations that are under the control of meristematic activity and element

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stoichiometry so that neither carbon nor nutrient shortage are reflected in active tissue traits and productivity. One of the big surprises is that these adjustments are so perfect that full-cover alpine plant productivity calculated per unit of active growth period is not inferior to that of most other biomes, provided moisture limitation does not come into play (Chap. 15). The 'time window for growth' emerges as the globally unifying principle that rules plant life in humid terres trial systems, with physiological adjustments mitigating the remaining thermal constraints within that 'window of opportunities'. This book illustrates the low temperature effects on plant life and the associated cellular and developmental responses. In essence, successful alpine plant life results from (1) microclimate engineering (plants are 'small by design'), (2) controlled development (phenology, life history) and (3) stress-physiological adaptations to resist extremes. The dependence on the latter is co-controlled by the second.

Alpine plant life, in essence, means mastering microlimate, timing of development, and stress tolerance. The snowbed plant *Soldanella pusilla*, here in 2440 m asl in the Swiss Alps, is a master of all three

Studying plant life at the low temperature limit can substantially contribute to basic plant sciences and open avenues of thinking, that might have been overlooked under less demanding environmental conditions. For example, my attempt at arriving at a functional explanation of the lower (warm) edge of the alpine life zone required an explanation of the upper tree limit, the global alpine treeline phenomenon (Körner 2012, Chap. 7). The outcome led to questioning the traditional way of viewing carbon relations as a central component for understanding plant growth in general (Körner 2015). The simple reason why trees reach an upper range limit beyond which alpine plants do well is their stature that evolved for light competition, but becomes a fatal handicap in a cool atmosphere (Fig. 7.9). To make a living above treeline requires (1) effective decoupling from ambient air temperature by small plant size and (2) in seasonal climates, more rapid development, which leads to the dominance of herbaceous or graminoid life forms.

Along similar lines, I believe understanding species range limits will bring developmental biology to the front, a field ecologists are commonly not well trained in or are not aware of its decisive role (see the *Soldanella* case in Chap. 5 and Chap. 14). As an example of promising fields, I invite readers to also re-visit Chap. 16 and the papers of the group led by J. Wagner in Innsbruck who delved into so far unexplored terrain of embryogenesis and the earliest stages of a plant's life. After these steps are accomplished, what is it, that permits or prevents a seedling to establish? Once established, the 'clonal machinery of alpine plant life' is very robust against environmental changes. Thus, a future challenge of alpine plant ecology will be explaining species range limits on such developmental and stress-physiological grounds.

I want to close this epilogue with a provocation: for not a single alpine plant species we have a mechanistic explanation of its distribution and range limit. By all respect for pragmatic, statistical, that is, correlative approaches at large scale alpine plant biogeography, projections of future species distributions in a changing environment will require resolving the most fundamental question not widely addressed currently: what is it that determines a species' low temperature range limit? The value of such understanding goes far beyond predicting species distribution, because it touches upon the very basics of alpine plant life, but also of plant distribution in responses to temperature in general. It may need a similar multidisciplinary approach, as was the basis for explaining the low temperature range limit of temperate forest tree species (Körner et al. 2016) to develop such a future research agenda for alpine plants.

The data collected and discussed in this book are a starting point, with researchers who will hopefully be entering this 'new world' of alpine ecology requiring an excellent background in microclimatology, not currently provided in biology or ecology curricula. Weather station data are close to useless in any attempt at explaining alpine plant life. It was a lucky coincidence that I grew up in an academic environment established by W. Larcher in Innsbruck (Körner 2021), where it was a self-evident starting point to professionally document and understand the life conditions of alpine plants, or plants in general, *in situ*.

References

Körner C (2012) Alpine treelines. Springer Basel

Körner C (2015) Paradigm shift in plant growth control. Curr Opin Plant Biol 25:107–114

Körner C (2021) Tools shape paradigms of plant environment interaction. Progress in Botany, in press

Körner C, Basler D, Hoch G, Kollas C, Lenz A, Randin CF, Vitasse Y, Zimmermann NE (2016) Where, why and how? Explaining the low-temperature range limits of temperate tree species. J Ecol 104:1076–1088