1   Plant ecology at high elevations

Plants respond to the harsh alpine environment with a high degree of specialization, the structural and functional aspects of which this book aims to explore. Palaeorecords suggest that life on land started out in sheltered, warm and moist environments, and gradually expanded into more demanding habitats where water is rare, thermal energy is either low or overabundant or where mechanical disturbance is high. More than 100 million years ago, when the large, hot deserts of the Cretaceous period where formed, coping with drought became a matter of survival in higher plants. Why is this of relevance here? Because survival of both drought and freezing temperatures requires cell membranes which can tolerate dehydration. When plant tissues freeze, ice is first formed in gaps between cells, which draws water from protoplasts (see Chap. 8). A link between the ultrastructural and molecular basis for freezing tolerance and the **evolution** of dehydration tolerance of biomembranes has therefore been suggested (Larcher 1981). Plant survival in cold as well as hot "deserts" – the two thermal extremes on the globe – thus may have common evolutionary roots, although life under such contrasting thermal conditions requires many additional, rather different metabolic and developmental adaptations. The ability to survive **low temperature extremes** opened the highlands of the earth to plants. The Tertiary (and still ongoing) uplift of mountain ranges strongly accelerated the evolution of alpine taxa (Billings 1974; Agakhanyantz and Breckle 1995). Embedded in different floras of the world, high mountains became both highly fragmented refugia and corridors of cross-continental migration, and often bear plant diversities richer than those in their surrounding lowlands (Körner 1995a; Barthlott et al. 1996; Chap. 2 and color Plates 1–3 at the end of the book).

The concept of limitation

Life in high mountains is mainly constrained by physical components of the environment (Fig. 1.1) and some high altitude plant specialists can survive incredible "extremes", for example dipping in liquid nitrogen. Some species manage to grow at altitudes of 6000 m (Webster 1961; Grabherr et al. 1995; see Chap. 2). The study of traits which enable plants to live in such climatic extremes has fascinated generations of biologists, but what is an extreme? Once the ability to cope with environmental extremes has evolved, such extremes become elements of "normal" life. If we move genetically adapted plants to what – from our human perspective – might be less extreme, most of these specialist plants would either die or would be suppressed by species native to the new habitat. Hence, in an ecological context, the concept of **"limitation"** becomes problematic (Körner 1988b). The term emerged from agronomy, where limitation was defined as a limitation of biomass production when compared with some maximum value that might be achieved with all resource limitations and environmental perturbations eliminated. However, in nature mass production only matters if it contributes to survival and reproduction, hence **fitness**. In so-called limiting environments, the enhancement of "limiting" resources or the removal of physical constraints

Fig. 1.1. Fit to survive and reproduce under demanding environmental conditions (*Ranunculus glacialis*, Alps 2600 m)

(stress) may stimulate (in the short term) growth and reproduction, but in the long term, may eliminate an organism from its previously more "limiting" habitat by competitive replacement. Environments are only limiting to those which are not fit.

The ability to cope with specific environmental demands can be achieved in three ways: (1) by evolutionary (phylogenetic) **adaptation**, (2) by ontogenetic **modifications**, which are non-reversible during the life of an individual (or its modules such as leaves or tillers) but are not inherent, or (3) by reversible adjustment, often termed "acclimation" or **modulation**. If, by any of these adaptive mechanisms, a plant achieves the ability to cope with the demands of its environment and successfully reproduces, it is fit – which by itself says nothing about the adaptive mode employed. Natural selection usually sieves for genotypic fitness. Populations of species with particular fitness for life in a particular environment are called "ecotypes" (Turesson 1925; Clements et al. 1950; Hiesey and Milner 1965). The history of the ecotype concept is closely linked with high mountain plant ecology (Billings 1957). High and low

altitude provenances of plants of the same species were the first for which clear ecotypic differentiation was demonstrated (e.g. Engler 1913; Turesson 1931; Clausen et al. 1948; Clements et al. 1950), and evidence for altitude ecotypes dates back to the last century (see Langlet 1971).

Altitude specific **ecotypes**, however, are only halfway to speciation. Though ecotypic differences within a species may be larger in some cases than differences among certain species, in the long term, it is the higher taxon difference at the species or even genus level that sets the strongest contrast between alpine and lowland specialists. Specialists exclusively found at high altitudes will more likely reflect a high degree of "adaptation" in their characteristics, and hence can be expected to behave as more typically "alpine" than plants which radiate from lower elevation centers to high elevation outposts (Gjaerevoll 1990). However, it will be demonstrated in this book that even specialist species with a narrow high altitude range are weak indicators of life zone specific behavior. The reason for this is the large structural and functional diversity that is found among plant species even at highest altitudes (Körner 1991). It is the habitat (altitude) specific community of species and the relative frequency of traits among those species that bears the most solid message with respect to **life zone specific adaptive responses** (cf. Billings 1957). Provenances or ecotypes of single species from a wide altitudinal range, extending far beyond the zone of greatest abundance, have the advantage of close taxonomic relatedness, but may be "Jacks of all seasons", and hence are less likely to bear the most characteristic features of the highest life zone of plants (Fig. 1.2).

These views of limitation, adaptation and life zone specific responses governed this synthesis, which adopts a **comparative approach** across large geographic and altitudinal scales and large groups of species. Wherever possible, consideration of **frequency** distributions of traits among species or community means rather than single species data are given priority. Given the taxonomic and micro-habitat diversity found in the alpine zone, monospecific studies are at risk to reflect
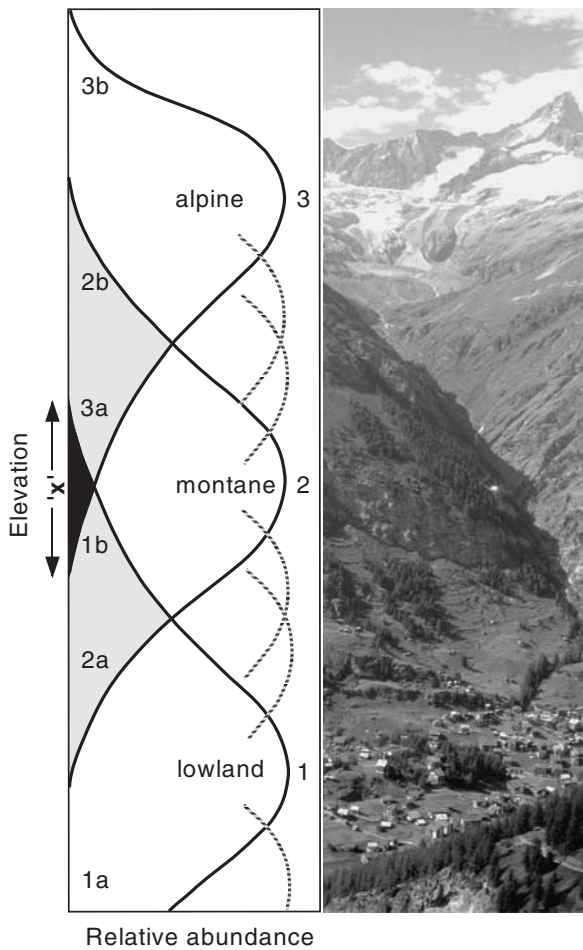
Fig. 1.2. Abundance ranges of different plant species or groups of plant species (*1, 2, 3*) or ecotypes of species (*1a,b; 2a,b; 3a,b*) along an altitudinal gradient. Ranges of maximum abundance do not necessarily reflect physiological optima but are simply centers of distribution. The comparative study of *1b* vs *1a*, *2b* vs *2a* and *3b* vs *3a* has the advantage of taxonomic (and possibly functional) relatedness and the disadvantage of comparing distribution tails (ecotypes from marginal habitats) rather than plants from the center of their range. In contrast, comparisons of plants with abundance peaks in the center of environmental antipodes (e.g. *3* versus *1*) are more likely to hit strong, life zone specific attributes, but taxonomic, and possibly functional diversity needs to be covered by comparing data for whole communities. Both approaches have been used in the past. For some questions, comparisons within overlapping zones, in particular the "*x*" zone bear a lot of scientific potential, but this has been explored to a lesser extent

curiosity rather than more general principles, even though the curiosity by itself may be a scientific jewel.

A regional and historical account

Research on functional ecology of alpine plants has a century-long **history,** and has its roots in comparative plant geography. By 1997 I had recorded approximately thousand publications dealing with functional aspects of alpine plant life and treeline biology (the phytogeographic and taxonomic literature on alpine plants is at least twice as large). The following brief and necessarily incomplete historical overview may assist readers in spotting some key references for geographic regions of interest. The later chapters are not structured by geography but by ecological topics. Where adequate, most recent examples have been used, which allow tracing references to earlier work. Figure 1.3 illustrates the geographical distribution of alpine plant research as reflected by the number of publications.

The pre-World War II research in alpine plants was almost exclusively conducted in the **temperate zone of Europe**, more specifically the Alps and the southern Scandes. The earliest scientific description of the elevational change in vegetation, the first mountain monograph of the world, is *Descriptio Montis Fracti* by K Gessner, who climbed Pilatus (Luzern, Switzerland) in 1555 and drew a rather precise picture, still valid today (Grabherr 1997, Zoller 2000). Possibly the first experimental attempts were those with transplants by Naegeli (mid 19th century from the Alps to Munich) and by Kerner (1869) from low altitude to alpine altitudes in Tirol. Interestingly, both these tests were not very successful. Most of Naegeli's alpine plants died at the "more favorable climate" at low altitude and also Kerner's lowland plants had obvious difficulties at the treeline, which led him to conclude that there must be an inherent (genetic) component associated with plant adaptation. From his famous reciprocal transplant experiments in the French Alps and
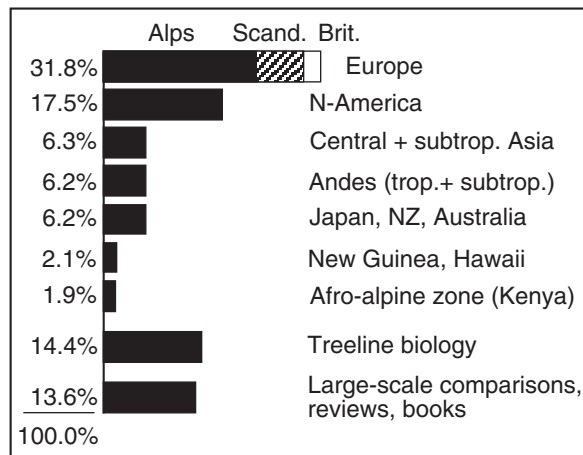
Fig. 1.3. Statistics of the geographical distribution of published research on the functional ecology of alpine plant ecology (evaluation of 800 publications). Publications on treeline biology are given in bulk. This survey does not include: geobotanical or floristic literature, papers on high altitude meteorology and climatology, soils, and conservation issues. Also work documented in the form of PhD or masters theses, institutional reports and publications in regional print media have been disregarded, because their inclusion would have biased the assessment toward the scientific environment of the author

Pyrenees, Bonnier (1890a, 1895) concluded instead that the environment has an overwhelming morphogenetic influence. Bonnier was the first to note with surprise (and by using incredibly simple devices) that the photosynthetic capacity of alpine plants is comparatively high. This conclusion matched well with the results of a broad leaf anatomical survey in alpine plants conducted during the same period by Wagner (1892) in the mountains around Innsbruck.

Following a first synthesis of knowledge by Schröter (1908, 1926), Swiss and Austrian researchers then took a lead in the more physiologically oriented alpine plant ecology for the first half of the 20th century. It was Senn (1922) and his student Henrici (1918) in Basel, who performed (in the Swiss Alps) the first reliable measurements of photosynthesis, transpiration and growth in alpine plants. Later, the Innsbruck group of Pisek (see his review in 1960) produced a large body of

evidence on temperature and drought resistance and many aspects of gas exchange in the major functional groups of plants at and above treeline. This research found a post-war continuation in treeline and subalpine research (e.g. Pisek and Larcher 1954; Friedel 1961; Tranquillini 1964, 1979) and in studies of a wide range of aspects of physiological ecology of alpine plants including high altitude extremes (Cernusca 1976; Moser et al. 1977 and the reviews by Larcher 1980, 1994, and Körner and Larcher 1988). As part of the International Biological Program, Larcher's group conducted the first process oriented, ecosystem research in the alpine zone (Larcher 1977) with follow up projects in the Man and Biosphere Program (Cernusca and Seeber 1981; Cernusca 1989). Alpine research in Scandinavia, which includes the transition to the arctic, and in Scotland, Europe's most humid alpine outpost, contributed almost one third of the current European literature on alpine plant life (e.g. Turesson 1925; Callaghan 1976; Wielgolaski 1975; Gauslaa 1984; Dahl 1986, Sonesson et al. 1991 for Scandinavia; Woodward 1983; Friend and Woodward 1990; Grace 1987 as examples of the work in Scotland).

After the genecological experiments with Californian alpine plants (Clausen et al. 1948), physiological ecology of alpine plants became a leading domain in the **temperate zone of North America** as well. Decker (1959) and Billings et al. (1961) were the first to test alpine plants under contrasting CO_2 concentrations, and, among other aspects, the physiological characterization of alpine ecotypes by Billings and Mooney (see their review in 1968) became a classic in plant ecology. Many other functional aspects of alpine plant ecology including reproductive biology have been studied in the following years by students of Billings (see his summary in 1987) and Bliss (1971, 1985; review by Campbell 1997). Caldwell (1968) pioneered research on solar radiation effects, including UV, water relations were studied by Ehleringer and Miller (1975) and others. At and above the Rocky Mountains treeline, a number of studies on plant nutrition and gas exchange have been conducted more recently

(e.g. Bowman et al. 1993; Hamerlynck and Smith 1994, a synthesis by Bowman et al. 2001).

Beginning in the 1930s, CO$_2$-gas exchange and water relations of alpine plants were studied in **temperate central Asia** (primarily in the Pamir and mostly published in Russian) by Blagowestschenski (1935), Zalenskij (1955), Semichatova (1965), Sveshnikova (1973), Izmailova (1977); later extended to questions of assimilate allocation, plant nutrition and developmental aspects by Agakhanyantz and Lopatin (1978). Most recently Pyankov et al. (1992) surveyed C4-species in high altitudes. In the 1970s eco-physiological and eco-climatological work was taken up in the Central Caucasus (e.g. Nakhutsrishvili 1976; Nakhutsrishvili and Gamzemlidze 1984) followed by the project by Rabotnov (1987) in the northwest Caucasus. For more recent work from the Caucasus, see Onipchenko and Blinnikov (1994), Tappeiner and Cernusca (1996) and Nakhutsrishvili 1999. Shibata (1985) reviewed work done in the **Japanese alpine zone** and examples of more recent work are the papers by Masuzawa (1987), Shibata and Nishida (1993) and Kikuzawa and Kudo (1995). Alpine plant research in the **temperate zone of the Southern Hemisphere** is exemplified by the work of Mark (1975) in New Zealand, Costin (e.g. 1966) and Slatyer (e.g. 1976, 1978) in the Snowy Mountains of southeastern Australia.

Functional ecology of alpine plants in the **subtropics and tropics** is largely underrepresented in the literature (Fig. 1.3.), and a substantial fraction of observational material collected did not find its way into easily accessible publications. In part this had to do with the difficulties for field work in tropical alpine conditions, and the resulting often incomplete data sets which did not meet the standards of (temperate zone) journals. Furthermore, priority of alpine research in these regions, had to be given to documentary work on the flora and life conditions, since most often not even the simplest base data were available. Examples of early observational material date back to Schimper (1898; see also Schimper and von Faber 1935), with the first detailed functional analysis of a **tropical** alpine vegetation by Hedberg (1964) and Hedberg and

Hedberg (1979). Approaches of more geobotanical emphasis are those by Vareschi (1951); Troll and Lauer (e.g. 1978) and Walter and Breckle (1991–1994 volumes); for new references for Africa (Kenya, Tanzania) see Hemp (2002) and Beck et al. (2002). Experimental work in the modern sense remained restricted largely to three truly alpine areas in the tropics: (1) The Páramos of Venezuela, with studies on gas exchange, freezing tolerance and growth forms (e.g. Larcher 1975; Baruch 1979; Goldstein et al. 1985; Meinzer et al. 1985; Rada et al. 1987; Smith and Young 1987; Monasterio and Sarmiento 1991; and comparative work in tropical Northern Chile (Arroyo et al. 1990; Squeo et al. 1991), (2) the afro-alpine vegetation on Mt. Kenya (e.g. Schulze et al. 1985, Beck 1994), and (3) Mt. Wilhelm in New Guinea (e.g. Walker 1968; Hnatiuk 1978; Körner et al. 1983). Syntheses of tropical-alpine plant ecology with individual contributions from all major tropical high mountain regions were edited by Vuilleumier and Monasterio (1986) and Rundel et al. (1994).

In the **subtropics**, again most research is from three areas, the alpine zone of the northwest Argentinan Andes (e.g. Ruthsatz 1977; Halloy 1982, 1991; Geyger 1985; Gonzalez et al. 1993), the southern Himalayas (e.g. Purohit et al. 1988; Pangtey et al. 1990; Sundriyal and Joshi 1992; Terashima et al. 1993) and the special island situation of Hawaii (Ziska et al. 1992; Sullivan et al. 1992; Lipp et al. 1994).

Introductions to alpine plant ecology **with a global perspective** are contained in Ives and Barry (1974); Franz (1979; a general overview, covering plants, animals as well as soils), and in the relevant chapters of the Walter and Breckle series (1991–1994). Klotz's (1990) and Archibold's (1995) books contain comparative overviews on alpine vegetation. Reviews on alpine plant diversity and its causes are contained in Chapin and Körner (1995). Functional aspects of the treeline problem have been reviewed by Wardle (1974); Tranquillini (1979); Grace (1989) and Körner (1998). The ecophysiology of alpine plants was reviewed in the above mentioned articles by Billings and Mooney, Bliss, Larcher, and Körner