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# 1 High elevation treelines

There are environmental constraints common to all high mountains that prevent tree growth beyond certain elevations and yield terrain to low stature alpine vegetation. This margin is called the ‘alpine treeline’. Trees may be absent from potential treeline elevations because of local peculiarities of the environment, a regional lack of capable species, or a multitude of disturbances, including those by humans. This volume aims at exploring the biological reasons for natural treeline formation with a global perspective.

As a prelude, I refer to Hoffmann’s (1876) reasoning about plant performance and temperature. Hoffmann worked in Giessen, Germany, when he phrased the issue in a timeless manner (my free translation): ‘At any given location there is a given amount of “warmth”. In as far as vegetation is established through the formation of cells, it represents the translation of warmth into organic structures, just as leaves transform solar energy into chemical building material’. Nearly 150 years ago, Hoffmann made a clear distinction between growth and carbon capture that we might have wished to see appreciated more often in later years.

## 1.1 The task

The upper margins of tree distribution in mountains around the world have attracted scientists for a long time. One of the earliest written accounts was possibly Conrad Gessner’s description of the forest limit in the front ranges of the Swiss Alps in 1555, and high elevation forest limits played a prominent role in Alexander von Humboldt’s global vision of biogeography (Fig. 1.1). Humboldt (Humboldt and Bonpland 1807) very clearly saw the treeline as a global phenomenon, a life form

boundary (Chap. 2) that he used as a common bioclimatological reference (see Chap. 5). In his still valid view of the world, all other elevational vegetation belts are positioned relative to this single most prominent reference. Given all the attraction this phenomenon had received, it is not surprising that a very rich literature had accumulated, with possibly close to 1000 individual articles, about 40 overview articles and ca. 10 books. So why another attempt at a synthesis? In the following I will try to explain the motives and aims of this undertaking.

Treeline or timberline (for definitions, see Chap. 2) research went through **waves of research cultures**. The early phase was phenomenological (e.g. Schröter 1908), and culminated in Däniker’s (1923) interpretation of the patterns he saw in the European Alps. Although he had almost no data, and all his reasoning was based on comparison and plausibility, it seems his visionary conclusion that tree growth becomes limited by lack of warmth came closest to what this book eventually will arrive at, however, based on a lot of data from around the world.

It was in the early 1930s when experimental approaches came in use and methods became available to measure physiological traits. This is also the time when, to my belief, a lot of confusion entered the field, not because measurements were faulty, but simply because they tied up people with their sites and specific methods. The greater the local efforts, the more particular interpretations became, and the further away from global explanation they carried the debate. One of the classics of this era was the then common idea that treelines are formed because of winter desiccation (Sect. 10.4). With a broader view at the mountains of the world, one would never have arrived at such a conclusion, although there are a few places on the planet where harsh



Fig. 1.1. Global plant formations as seen by Alexander von Humboldt. Note, the latitude specific elevation of the forest limit (Humboldt 1845–1862)

winter conditions may cause such damage as for instance in the central Alps and parts of the Rocky mountains. It took nearly half a century until Tranquillini (1979) presented the first synthesis based on empirical data - still a largely European, temperate zone picture, because this was the area from where most of the data came. Thanks to this **treeline classic**, growth itself became a focal point once more (see Däniker's paradigm, above) and other explanatory approaches, including photosynthetic performance and low temperature resistance became known as uncritical or not tree-specific, points confirmed several times in more recent years for other parts of the globe (Chaps. 10 and 11).

The third wave, rooting in Humboldt's tradition, somewhat overlapping with the second, started during World War II with Carl Troll's biogeographical approach (e.g. Troll 1973a). Troll's comparative view re-introduced the broader picture and emphasized the global nature of the treeline phenomenon. Arriving at quantitative biogeographic data from around the globe (Hermes 1955) and testing climatological correlates (e.g. Lauer 1985), this school of researchers drew the framework into which experimental work needed to become integrated, abandoning generalizations from region specific patterns and observations, and **adopting comparative approaches** at large scales. Unfortunately, this integration hardly happened. For the rest of the last century, the two schools co-existed (the ecophysiological, tied to sites, and the geographical, descriptive/correlative), with hardly any linkages. Biogeographic explanations became more varied as more places were considered

and the real mechanisms remained presumptive. Since more likely causes were not distinguished from less likely ones and local phenomena got mixed up with global ones, we arrived at an 'everything matters' philosophy, which I consider an end point of scientific endeavour, because it dispenses the experts from qualified judgement and ranking. Not surprisingly, the discussion drifted further away from understanding treelines as we were in Däniker's days. Experimentalists remained occupied by their site's and species' peculiarities (both commonly cool temperate) and missed out the comparative elements, so self-evident to most bio-geographers.

This is a classical 'the blind men and the elephant' situation. According to this old parable, believed to come from India, a few blind men were permitted to touch an elephant and then dispute what it is like. One was given the tail to touch, others touched the ear, the leg, the trunk. . . Easy to imagine how the story goes on. The often seemingly conflicting views about the causes of treeline in reality emerge from a narrow perspective, from a sort of enlarging glass view, at scales at which a multitude of factors may indeed interfere, with the more basic drivers becoming overlooked. This book will take a wide-angle lens view, not ignoring these micro-facets, but placing them in a larger, **global context**, scales at which a few tenths of metres of local variation in treeline elevation do not matter.

Had Willhelm Schimper not died from a tropical disease at an early age in 1901, after his third expedition, soon after he became a professor of Botany in Basel, we might have seen a different history.

Schimper (1898) was among the first who realized that experimental ecology must become comparative and adopt a global view in order to explain the big phenomena which drive the biosphere, such as cross-continental high elevation tree limits. In his concept of 'plant geography on a physiological basis' answers to those overarching questions were never expected to emerge from a particular site's data. Most of the high quality experimental works on treelines during the past decades remained spatially isolated and confined to temperate zone mountains, with a few notable exceptions.

When I started to consider writing such a synthesis about 15 years ago, this was when the culmination of experimental ecology in this field was over. A great deal of unanswered questions remained, many rather obvious ones remained hardly addressed. Most trivial ones were not even asked, such as 'when exactly do trees build new cell layers in their stems'. Reading the steady flow of new publications it became increasingly obvious that there is a need to separate local phenomena and their causes from global patterns and their common drivers. If there was a motto for this enterprise, it was this **separation of peculiarity from generality** (Fig. 1.2).

This volume aims at a **theory of treeline formation which stands the test across the globe's** mountains, irrespective of local, small scale modulating forces, which became dominant in much of the concerned literature. As Humboldt and many others have shown, there is no better bio-climatic reference than the high elevation treeline, which thus permits latitudinal comparisons of biota. Using climate rather than elevation, a mountain forest in New Guinea at 3700–3900 m elevation becomes climatologically comparable to a mountain forest in the Alps at 2000–2200 m elevation, with the two upper limits representing the respective treelines, irrespective of the many still existing environmental differences, those in seasonality in particular. The climatic causes for high altitude tree limits need to be identified and the processes which cause the change from tall tree to low shrub and grass are to be explained. We need to find out which drivers and processes can explain the

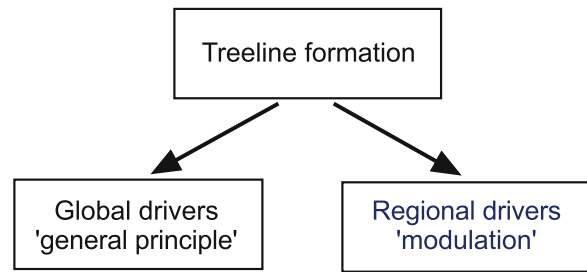


Fig. 1.2. Global *versus* regional drivers of forest and tree limits. Global drivers are acting on all mountains and have a bioclimatic foundation, whereas regional drivers vary from location to location and include site-specific (not elevation-specific) disturbance regimes (see Fig. 1.3)

relatively sharp boundaries in an otherwise gradually changing environment with increasing elevation (Fig. 1.3). And we need to answer **what makes trees different from non-tree plants** that strive at much higher elevations.

*Alpine Treelines* adopts a similar approach to *Alpine Plant Life* (Körner 2003a). Each of the thematic chapters will address a specific facet of tree life and will start with a short theoretical introduction, followed by findings in the respective fields, and closing with the main messages. The sequence of chapters was chosen to start with conventions and definitions (Chap. 2) and with biogeographic and bioclimatological aspects (Chaps. 3–5), followed by chapters on morphology, growth, development and evolutionary traits (Chaps. 6–8). Reproductive biology and young life stages are treated in Chap. 9, followed by more physiological chapters on freezing tolerance, water, nutrient and carbon relations (Chaps. 10, 11), and closing with a summary of the current understanding and accounts of past and future treelines (Chap. 12). None of these themes will be reviewed exhaustively, but will be addressed by examples which illustrate the main lines of knowledge. As will be explained in Chap. 2, this book will strictly **refrain from dealing with issues which are not specific to high elevation life conditions**. The inclusion of such themes in earlier attempts had already produced a lot of confusion. Thus, forest clearing by man, effects of fire or drought, etc. are not an issue here, because these

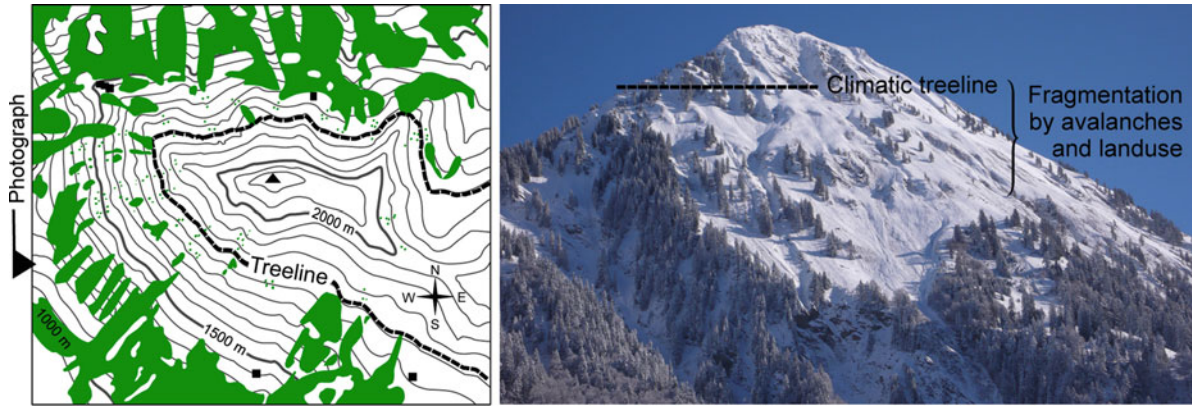


Fig. 1.3. Elevation-specific ('treeline') and other, non-elevation-specific determinants of forest margins at high elevation, together, are forming the patterns of forest and tree limits seen in the landscape. The scientific challenge is to separate the elevation-specific biological drivers from other drivers in order to arrive at a robust treeline theory (Üntschenspitze, Schoppernau in Bregenzerwald, Austria)

factors can operate anywhere on the globe, are not high elevation specific, and cannot contribute to a global treeline theory based on biological principles. If there were no such biological foundations, no global pattern could emerge as we see it, simply, because it is impossible that disturbances such as the ones mentioned above would be the same in all mountains. It will be a major task to identify globally common determinants of treeline formation and how these act.

## 1.2 Previous works

In this section I will mention a few key references meant to help readers accessing further global or regional treeline works. I will start with a few general texts and then comment on regional accounts by continent. Inevitable some of these works belong to both categories, and more detail will be presented in the respective chapters.

Readers who seek a more general illustration of the treeline landscape and conditions will find plentiful information in richly illustrated volumes such as those by Holtmeier (2009), Burga et al. (2004) and Nagy and Grabherr (2009). Though dominated by findings from the European Alps, the earliest attempt at a **general synthesis** is that

by Schröter (1908, 1926) which possibly inspired Däniker (1923) to his treeline theory based on growth and thermal energy. **Global comparisons** have been presented by Troll (1961, 1973a,b), Troll and Lauer (1978), Holtmeier (1974, 2000, 2009), Wardle (1974, 1993, 1998), Armand (1992), Miehe and Miehe 1994, Cabrera (1996), Körner (1998, 2003a), Walker (2000 for arctic treelines), Broll and Keplin (2005) and Crawford (2008) all pointing at the characteristic features of trees at treeline and environmental impact on tree stature as well as climatic relationships. General accounts on treeline dynamics have been published by Glock (1955), Ives (1978) and Slatyer and Noble (1992).

Specific **bioclimatological works** with a cross-latitude perspective started with Daubenmire (1954) and Hermes (1955), the latter successfully correlating latitudinal treeline elevations with snowline elevations. The warmest month 10°C isotherm came into discussion as a treeline correlate (Brockmann-Jerosch 1919; Köppen 1919, 1936). A first in-depth account of the climatological implications of the 'massenerhebungseffekt' was published by De Quervain (1904) based on data for the Alps. The general relatedness of treeline with climate was also assessed by Glock (1955), Lauer (1985) and Körner (1998, 2003a, 2007a). Jobbagy and Jackson (2000a) used estimates of annual



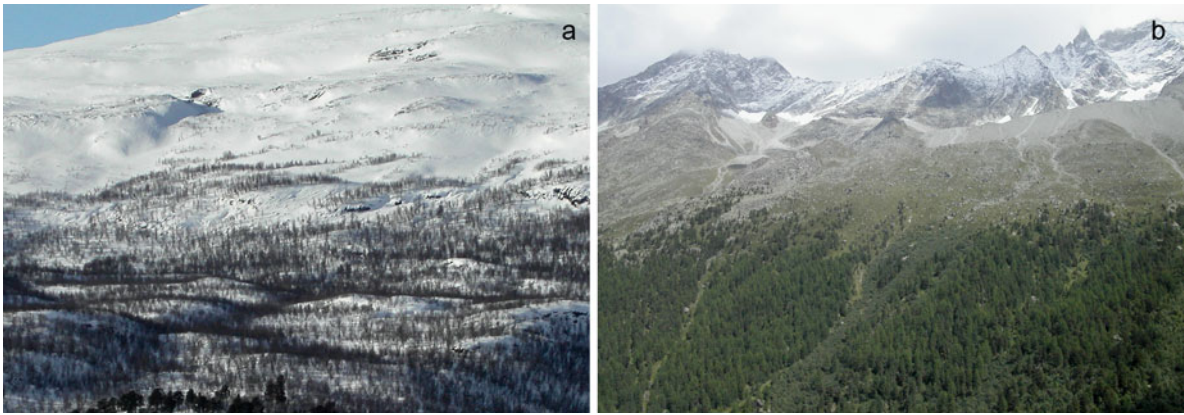


Fig. 1.4. Treelines in Europe. a Abisko, north Sweden, 650 m, *Betula pubescens*. b Arolla, Valais, Swiss Alps, 2350 m, *Pinus cembra*

mean temperature to define treeline positions, and Körner and Paulsen (2004) presented a global comparison of *in situ* measured treeline temperatures. Recently, Smith et al. (2009) discussed facilitation phenomena related to the microclimate in regrowth stands.

The **experimental ecology** literature culminated in a first general synthesis by Tranquillini (1979) based on data for the temperate zone, largely the Austrian Alps, followed by two conference volumes by Benecke and Davis (1980) and Turner and Tranquillini (1985), with data from both hemispheres. Grace (1989), Stevens and Fox (1991) and Sveinbjörnsson (2000) discuss possible biological causes of treeline formation based on literature data. Körner (1998, 2003a) summarized published evidence for the six major hypotheses on treeline formation. An account of empirical advances since Tranquillini's review for the Alps was published by Wieser and Tausz (2007).

Reviews on **palaeoecological works** with a broad comparative emphasis have been written by Wijmstra (1978), Innes (1991), Flenley (1998), Miehe et al. (2006) and general aspects of **climatic change** on treelines have been discussed by Grace (1989), Paulsen et al. (2000), Grace et al. (2002), Stottlemeyer et al. (2000) and Walther et al. (2005).

Regional overview articles have been published for all continents. For **Europe** (Fig. 1.4), the rather detailed assessment of treeline elevations (and its history) for the **Alps** by Imhof (1900) was followed by Schröter's (1908) synthesis and Brockmann-Jerosch (1919) and Friedel's (1967) work on treeline elevations and their climate relatedness, with the recent advances in ecophysiology reviewed by Wieser and Tausz (2007). Ellenberg (1963) and Ozenda (1997) provided a general account of vegetation belts, including the treeline. For the **Scandes**, I refer to Treter (1984) and Kullmann (1998 and earlier works) and for the **British Isles** to Grace (1989). Jenik and Lokvenc (1962) compiled the literature for **Eastern European** mountains. Dendroecological and palaeoclimatic works for the Alps can be found in Frenzel (1977, 1993, 1996), Rolland et al. (1998), Burga and Terret (2001), Tinner et al. (1996), Tinner and Theurillat (2003) and Rossi et al. (2007), for the Scandes in Sonesson and Hoogesteger (1983), Kullmann (1990), Birks (1996) and Zetterberg (1996).

For the northern part of **Asia** (Fig. 1.5), Malyshev (1993) reviewed treeline elevations; literature for the central **Himalayan** forest limit was compiled by Singh et al. (1994), and for Tibet by Bosheng (1993) and Miehe et al. (2002, 2007). The treeline positions in continental east Asia and the relevant literature were discussed by Ohsawa (1990) and

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