

2 HISTORY AND PRESENT STATE OF TIMBERLINE RESEARCH

The upper timberline is the most conspicuous vegetation limit in high-mountain areas of all continents, except for the Antarctic. Timberline is also an important ecological boundary, marked by a change in site conditions and plant communities when crossing the forest limit. For example, above the closed forest topoclimatic conditions, soil distribution patterns, intensity of soil erosion, etc. are totally different from the forest belt. This also holds true for the habitat conditions of the forest-alpine tundra ecotone. It is characterized by a greater habitat variety compared to the closed mountain forest. The fact is that no other vegetation limit has a comparable effect on the high-mountain environment, making it all the more astounding that scientists have addressed timberline studies only relatively recently. In general, timberlines that have been disturbed by human impact are best investigated because access mostly is relatively easy.

2.1 Early timberline research

The earliest reports on timberline or treeline are usually based on more or less accidental observations, usually originating from general regional and local geographic studies. They mostly provide general remarks to the effect that mountain forests end at a certain altitude. The first reliable data on the altitudinal position of timberline are hardly older than 200 years (e.g., Hacquet, 1779; Zschokke, 1804, 1805, 1806; Kasthofer, 1818, 1822). Systematic timberline research began about 150 years ago. Early timberline research was reviewed by Imhof (1900), Marek (1910), Däniker (1923), and Holtmeier (1965, 1974).

When it became apparent from the increasing number of observations that climatic timberline and tree line are mainly caused by heat deficiency, researchers began to focus on thermal conditions (Sendtner, 1854; Kerner, 1864/1865). Some authors (Supan, 1994; Drude, 1890; Andersson, 1902; Köppen, 1919, 1920) emphasized the conspicuous coincidence of the polar timberline and the 10°C-isotherm of the warmest month (July). Kasthofer (1822) and the brothers Schlagintweit and Schlagintweit (1854) first mentioned the positive effect of mass-elevation (mountain-mass effect, Merriam effect) raising the altitudinal limits of vegetation, snow, and also agriculture and human settlements. Later, the mass-elevation effect on the

position of the upper timberline (Imhof, 1900) and other altitudinal limits such as snow line (Jegerlehner, 1903), and upper limit of human settlement (Flückiger, 1906) was systematically studied. Enquist (1929, 1933) calculated the duration and thresholds of certain temperatures that he believed to be the factors controlling the altitudinal limits of timberline forming tree species. Moreover, some coincidence was found between the altitudinal position of timberline or tree line and mean temperature of the 3 or 4 warmest months (tritherm or tetratherm), and the total sum of temperature of the growing season. Alternatively, the use of degree-days (base 10°C) has replaced the use of isotherms when close correspondence between degree-days and major vegetation zones was found (e.g., Hopkins, 1959). Attempts were also made to discover whether timberline is correlated to the amount of precipitation, an idea that Maurer (1915) refuted.

Altogether, those studies were necessarily based on the interpolation of data from meteorological stations far distant from each other. This holds particularly true for the northern timberline. Thus, all these attempts should be considered as approximations by data available in those days. The correspondence that had been found between the altitudinal position of timberline and mean temperatures of the growing season, air temperature sums, etc., clearly reflect the influence of heat deficiency, although mean temperature cannot be considered a causal factor (Section 4.3.1).

The monographs of Imhof (1900) and Marek (1910) improved the knowledge on timberline considerably. Imhof was concerned with the timberline in the Swiss Alps, where he systematically studied the mass-elevation effect on timberline, while Marek (1910) did the same for the Austrian Alps. Finally, Brockmann-Jerosch (1919) provided a synthesis of the knowledge of that time, and instead of the effects of single climatic factors he considered the influence of the climate character on the position of timberline in a world-wide view. Almost 40 years later, the geographer Hermes (1955) published a comprehensive monograph, based on a thorough review of literature, on the upper timberline and its distance from snow line in the mountains of the world. There are many other local and regional studies on high-altitude forests, on the requirements of the tree species forming the timberline, on forest history, forest use, and others. Although mainly descriptive, they all have contributed to a better understanding of timberline.

However, they could not provide deeper insight into the ecological causalities controlling position, spatial structure, and dynamics of timberline. In this respect, Kihlman's monograph on the northern tree line on the Kola Peninsula (Kihlman, 1890) was more progressive. Even today it is surprising how he assessed the ecological conditions and the effects of tree line-affecting factors such as winter desiccation, for example, by careful observation and consideration. For the most part his hypotheses should become evidenced by experimental research half a century later.

2.2 Modern timberline research

In the Alps it was Däniker (1923) who first studied timberline with special regard to ecological conditions. Modern experimental ecological timberline research began in the 1930s with the studies of Pisek and Cartellieri (1939), Michaelis (1934a, b, c, d), Steiner (1935), and Schmidt (1936). Timberline research in the Alps was stimulated by heavy avalanche catastrophes that occurred during the winter of 1951/1952 and 1953/1954. The high frequency and the high destructiveness of the avalanches and also of debris and mud flows were attributed for the most part to deforestation of the mountain slopes by humans (alpine pastures, mining, salt works, etc.) and to the bad condition of the over-used and over-aged high-altitude forests. Kasthofer (1822) and Landolt (1862) already emphasized the protective function of mountain forests and their reports encouraged forest restoration in some areas. In view of the many destructive avalanches that had occurred in the two consecutive snow-rich winters in the middle of the 1950s, extensive research programs were initiated in Austria and Switzerland to create scientific fundamentals for assessment and appropriate, site-adapted management (microclimate, soils, physiology, regeneration, etc.) of the mountain forests up to the potential timberline. Research stations were established close to timberline in Switzerland (1959, Stillberg in the Dischma Valley, near Davos) and Austria (1953, Obergurgl). Particularly in those areas many experimental field studies on topoclimate, plant communities, soils, snow fungi, mycorrhiza, and on the ecology and aptitude of tree species for high-altitude reforestation were carried out.

Also, many local and regional studies on timberline were published in regional monographs or in journals and periodicals of botany, geography, and forest sciences. Moreover, many publications are concerned with more special aspects such as altitudinal shifts of timberline over the course of time, tending or restoration of the protective functions of mountain forests. Further information is provided by investigations on the distribution and ecological requirements of the timberline-forming tree species and high-elevation forest management. The recently published books on 'Nordic mountain birch ecosystems' (edited by Wielgolaski, 2001) and 'Plant ecology, herbivory, and human impact in Nordic mountain birch forests' (edited by Wielgolaski et al., 2005), constitute a very valuable reference and summary of the present scientific knowledge on these birch forests, although timberline itself is more casually considered. Timberline in the Swedish Scandes has been studied in particular by Kullman (see reference list in this book). Brandes (2007) has published a many-faceted thesis on timberline in the high-mountains of Greece. This thesis is a valuable contribution to a better understanding of the Mediterranean timberlines in general as it shows timberline physiognomy, altitudinal position and dynamics being influenced

more by natural factors than might be expected in view of historical human impact (pastoral use, fire, etc.) which affected timberline for thousands of years. Also, a great regional variety of timberline in the study area becomes apparent. Compared to the European Alps, no other mountain region has been covered by so many studies on the ecology of the timberline-forming tree species and on practical application of the results at high-altitude afforestation and restoration of mountain forests (Turner, 1985). However, hardly less numerous are the investigations of upper and northern timberline in North America and Scandinavia. Many of those studies are concerned with regional timberline dynamics as influenced by climatic fluctuations (references in Chapter 5).

In 1979 Tranquillini, a pioneer in experimental research on ecophysiology of timberline tree species, compiled the results of his own and others research in his book 'Ecological physiology of alpine timberline'. This book represents the state of the art at that time; it still is a good source for information and undoubtedly is most often quoted by English-speaking timberline researchers. Almost 30 years later, Wieser and Tausz (2007) edited a treatise on 'Trees at their upper limit' which continues the tradition of Tranquillini's timberline book. Unlike this book the new treatise is a cooperative work of nine experts. Although focussing mainly on the ecophysiological aspect of treeline in the European Alps it also includes altitudinal treelines on temperate mountains worldwide. The book gives a concise and thorough overview of the present state of knowledge on tree ecophysiology relevant to the altitudinal timberline in temperate mountains. However, the possibilities of transferring the results of experimental studies in laboratories or on field plots and of any other local investigations to other areas are limited, because of the great variety and heterogeneity of timberline. Even within a single mountain region, such as the Alps, we face problems in this respect due to the very locally varying site conditions. In particular, difficulties will increase in applying local results to timberline of distant mountain ranges, such as the Himalayas, for example (e.g., Miehe, 1982).

Altogether, the ecophysiological situation of trees growing at the upper timberline in the Alps, in other high mountains and in the Subarctic of North America and northern Europe can be considered the best investigated. Compared to these timberlines the knowledge on timberlines in the tropics is still fragmental (Miehe and Miehe, 1994, 1996). Recently, Schickhoff (2005) gave an extensive overview of the timberline in the Himalayas, Hindukush and Karakoram based on his own studies and a widely scattered literature on altitudinal position, physiognomy and floristics. Research on timberline ecological conditions in these mountain systems is still in its infancy. The same holds true for the timberlines at middle latitudes in the southern hemisphere, except for New Zealand. Most information refers to the East-African

mountains (Hauman, 1933; Fries and Fries, 1948; Klötzli, 1958, 1975, 1977; Hedberg, 1964; Coe, 1967; Plesnik, 1980; Bussmann, 1994; Miede and Miede, 1994, 1996, 2000), to Mexico and the South-American Andes (Troll, 1959, 1973; Beaman, 1962; Lauer, 1973; Klink et al., 1973; Lauer and Klaus, 1975a; McQueen, 1976; Klink and Lauer, 1978; Hueck and Seibert, 1981; Bauman, 1988; Hildebrand-Vogel et al., 1990; Seibert and Meinhofer, 1991; Jordan, 1996; Vogel, 1996; Wardle, 1998), and to New Guinea (Van Steenis, 1953; Hope, 1976; Löffler, 1979; Smith, 1980). Recently, Bader (2007) published a detailed treatise (doctoral thesis) on tropical altitudinal treelines with emphasis on the ecological processes and factors controlling spatial timberline patterns, physiognomy and dynamics. The studies refer to the South American Andes and to Haleakala volcano (Hawaii). Schweinfurth (1966, 1980) and in particular Wardle (1985a, b, c, 1991, 2007) investigated the timberline in New Zealand and also reviewed older studies. The less advanced exploration of timberline in the 'southern' mountain regions may be partly explained by the fact that pressures to restore high-altitude forests have not been as strong so far as in the Alps, for example. Actually, human impact (lumbering, grazing, burning, bark-stripping, etc.) on mountain forests in subtropical and tropical regions is continuously increasing due to rapidly growing population (Haffner, 1982; Schickhoff, 1995a, b, 1996; cf. Section 4.3.14.2). In a not too distant future restoration of high elevation forests might be the only way to prevent humans from the negative effects of man-caused forest decline.

Besides the extensive studies of Brockmann-Jerosch (1919) and Hermes (1955) there are only a few recent and relatively concise contributions comparing timberlines on a world-wide scale (e.g., Ellenberg, 1963; Troll, 1973; Wardle, 1974, 1993; Holtmeier, 1985b, 1989; Plesnik, 1991; Körner, 1998a, b, 2007b), some given in connection with a presentation of the ecological situation of alpine vegetation in general (Crawford, 1989, 2008; Körner, 1999).

Arno (1984) has provided the most comprehensive modern compilation. Although mainly referring to timberlines in North America and written for the general public it also is very useful to any scientist interested in timberline. However, the author refers almost without exception to literature written in English. Ohsawa (1990), Tuhkanen (1993), Malyshev (1993) and Miede and Miede (1994, 1996) provide outlines of timberline of larger regions, mainly with respect to the influence of thermal conditions on the timberlines.

Global climate change has a stimulating effect on timberline research as is reflected in the rapidly growing number of publications. In a series of publications, Körner and co-authors, for example, have revived the age-old discussion on the 'ultimate cause' of altitudinal treeline. They consider low mean temperatures in the rooting zone during the growing season or

all-year-round (at tropical treelines) to be the critical factor controlling directly worldwide treeline position (Körner, 1998a, b, 1999, 2003a, b for review; Paulsen et al., 2000; Hoch and Körner, 2003; Körner and Paulsen, 2004; Hoch and Körner, 2006; Körner, 2007b). This theory is considered applicable everywhere and to steer modern treeline research around to the supposed 'right' direction (e.g., Hoch and Körner, 2003).

Undoubtedly, a well-defined threshold soil temperature controlling tree-line worldwide would put out timberline researchers from the misery of inscrutable timberline complexity and would also make modelling the future timberline position a lot easier (see also Körner, 2007b). However, many uncertainties and inconsistencies are left (Section 4.3.5) and the discussion continues. Modelling treeline response and possible consequences of treeline advance to greater altitude and more northern locations has become a modern instrument to approach the timberline phenomenon (Chapter 6).