

TREES AT THEIR UPPER LIMIT

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Trees at their Upper Limit

Treelife Limitation at the Alpine Timberline

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Preface

As one of the most conspicuous transitions between very different types of ecosystems the alpine timberline attracted the interest of researchers for many decades. Obviously the life-form tree reaches its absolute limit and is constrained by the harsh environment. However, the nature of such constraints is less obvious and requires detailed ecophysiological analyses as exemplified in the chapters of this book. Only a clear mechanistic understanding of the timberline phenomenon will enable us to predict the potential impacts and changes caused by human activity and related global change in this sensitive region.

The contributions in the present volume deliberately concentrate on the timberline of the European Alps, but as numerous examples from places such as North America, New Zealand, or Australia, which are cited by the contributors, underline, the principles developed in this book can be applied to temperate mountain ecosystems all over the world.

We would like to use the opportunity to thank all our authors for their timely high quality contributions and are proud to have been able to enlist leaders in their field. On a more personal note, we would like to gratefully acknowledge the work of senior colleagues with whom we were lucky enough to cooperate and profit from their experience: D. Grill (Graz) used altitude gradients to investigate the stress physiology of spruce trees and was one of the first to highlight the role of antioxidants in plant defence. W. Larcher (Innsbruck) is regarded as one of *the* authorities in plant ecophysiology worldwide and developed many of his widely appreciated concepts from research at the timberline. The groundbreaking work by W. Tranquillini (Innsbruck) published in his book “Physiological ecology at the timberline” still forms the basis of every timberline research and also of this volume.

We also thankfully acknowledge the fruitful co-operation with the Springer team during all stages of the project, especially R Kanters and C Cotton.

The present book is designed to give a concise yet in-depth overview of the current state of knowledge in tree ecophysiology relevant to the alpine timberline. We hope that it is not only of use for more experienced re-

searchers, but also for students and early-career scientists who are already interested in timberline questions, and particularly for those who may become motivated to undertake their research in this field.

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1 Current Concepts for Treeline Limitation at the Upper Timberline

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1.1 Introduction

The upper timberline designates the upper elevational limit of forest and tree growth and survival on high mountains due to environmental constraints such as cold temperatures, drought, low nutrient availability, water logging, and stormy winds. Rather than being an abrupt boundary, the upper timberline usually forms an ecotone between the closed continuous forest below (i.e. the forest line), and the treeless alpine zone above (Däniker 1923; Wardle 1974; Tranquillini 1979; Slatyer and Noble 1992; Holtmeier 2003).

The timberline ecotone stretches from the *forest line* or upper limit of a continuous forest canopy to the *tree limit* which is the extreme upper limit of the occurrence of tree species. Within this transition zone above the closed forest canopy trees become stunted and upright trees can finally be deformed to *krummholz* due to climatic severity or the woody vegetation above the forest limit consists of *scrub*-like trees.

Kampfzone is another term for the upper timberline belt in recognizing the severe growth conditions that trees must face at their upper elevational limit. While the term *krummholz* designates environmentally dwarfed forms of tree species that become upright in favourable sites, the term *scrub* should only be applied to those timberline species, whose shrubby form is of genetic origin (Wardle 1974; Tranquillini 1979; Holtmeier 1993,

2003), as for example *Pinus mugo* a species commonly growing in rock gardens.

Thus, it is useful to define the tree limit as the upper limit of trees, krummholz, and shrubs higher than 2 m (Wardle 1974, 1981; Piusi and Schneider 1985; Ellenberg 1996). Such a minimum tree height ensures that the tree's crown is well coupled to the atmosphere and that trees are more exposed to the prevailing climatic conditions and are not completely covered by snow where snow occurs (cf. also Däniker 1923; Holtmeier 2003) when compared to low-growing vegetation such as dwarf-shrubs, alpine grassland, and meadows.

1.2 Altitudinal position of the upper timberline and its relation to climate

The upper elevational limit of tree growth represents a balance between abiotic and biotic factors (cf. also Scuderi 1987) in which the climate becomes increasingly less favourable and interacts with the tolerance of trees, determining their upper limit. The position of the upper timberline on a global scale has been described by several authors (Hermes 1955; Troll 1973; Wardle 1974; Franz 1979; Arno 1984; Körner 1998; Holtmeier 2003), usually considering latitude as a surrogate of temperature (Hermes 1955; Cogbill and White 1991; Körner 1998, 2003; Jobbagy and Jackson 2000). In both hemispheres the upper timberline rises from high latitude towards the subtropics, and then gradually declines in the tropical equatorial zone (Fig. 1.1). Moreover, the altitude of the treeline depends not only on latitude but also on continentality, especially in temperate interior zones of North America and Asia, where timberlines are nearly as high as those of the tropics (Fig. 1.1).

This is due to the “*Massenerhebungseffekt*” (mass elevation effect; Brockmann-Jerosch 1919), and thus causing a decreased temperature lapse rate and therefore also higher climatic and biotic zones on high and large land masses. This heating effect is also combined with a climate becoming increasingly continental from the front to the central ranges of mountain systems. Central ranges generally experience less precipitation, more sunshine, a shorter continuous snow cover, and less exposure to frontal winds than the outer rims. For example, in central ranges of the Austrian Alps the growing season can be up to 80 days longer when compared to outer ranges (Turner 1961). On isolated oceanic islands however, the upper limit of tree growth and survival is mainly controlled by edaphic factors rather than a (non-existent) “*Massenerhebungseffekt*”.

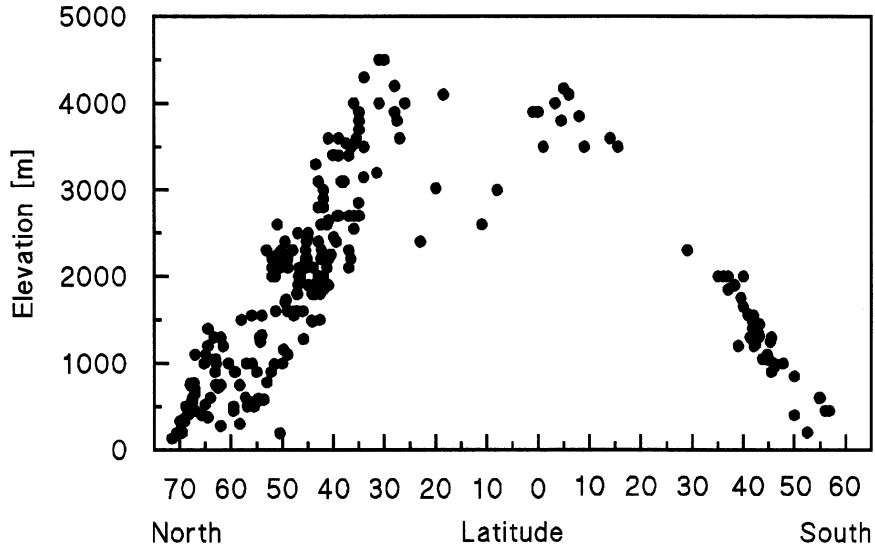


Fig. 1.1. The latitudinal position of the upper the treeline. (Redrawn after data collected by Hermes 1955; Wardle 1974; Franz 1979; Arno 1984; and Jobbagy and Jackson 2000.)

In the last century several authors have claimed that the upper treeline in the northern hemisphere (Daubenmire 1954; Holtmeier 1974; Grace 1977) and in New Zealand (Zotov 1938) corresponds to a mean isotherm of 10 °C of the warmest month of the year. However, one has to take into account that the growing season may range from 2.5 months at high latitude to 12 months in the tropics. Furthermore, winter snow cover is also a site controlling factor in the temperate zone but is missing in the tropics. Thus, on a global scale, the upper treeline approaches an elevation corresponding to a mean air temperature of the growing season ranging from 5.5 to 7.5 °C (Körner 1998, 2003; Hoch et al. 2002).

Climatic data are often derived from meteorological stations based at lower altitudes and temperatures are adjusted (in fact “scaled up”) to the upper treeline position using a certain lapse rate in the reduction of air temperature with elevation (cf. Tranquillini 1979; see also Chap. 2.1). Mean temperatures however, do not exist in nature and therefore such data should not be used as a causal factor for explaining the upper limit of tree survival, although they might be an indicator. This should also be taken into account when discussing threshold values for air temperature as well as mean soil temperature data (Daubenmire 1954; Körner 1998; Körner

and Paulsen 2004) as a surrogate for explaining the climate driven upper limit of tree life on a global scale.

Furthermore, meteorological data do not match the temperatures trees actually experience (Tranquillini and Turner 1961; Gross 1989; Friedland et al. 1992; Stirmbeck et al. 1993; Jordan and Smith 1994; Wieser 2002). Above ground tissue temperatures can be notably cooler during the night and considerably above air temperature during the day. Temperature effects on tree behaviour are complex and influence growth, germination, and metabolic processes. Temperature response functions are generally non-linear. High or low temperature extremes may cause heat or frost tissue damages and in the extreme even cause tree death. In addition, temperature also alters the physiological condition of trees and trees must be able to adapt. Additionally, outside the tropics this adaptation has to be synchronised with seasonal variations in temperature (Havranek and Tranquillini 1995).

1.3 Current concepts of upper tree life limits

Although on a global scale the upper limit of different tree species may vary with respect to site conditions, the upper limit is ultimately dependent on heat balance, which everywhere becomes increasingly unfavourable with rising elevation. Outside the tropics warm season temperatures rather than low temperatures during the cold season have been suggested to control the upper limit of tree growth (Troll 1973; Wardle 1974; Tranquillini 1979; Havranek and Tranquillini 1995). In temperate regions, trees become dormant during unfavourable cold periods and increasing frost shortens the period available for growth and development. Information on the actual length of the growth period can be obtained from tree phenological and physiological measurements. In a 6-year data set of ecophysiological analysis, Friedel (1967) showed that in the Central European Alps (2100 m a.s.l., Ötztal, Tyrol, 46° N, 11° E) *Larix decidua* has an average vegetative period of 128 days. Conditions at the timberline ecotone near Innsbruck (1950 m a.s.l., Klimahaus Research Station; 47° N, 11° E) are similar, where the 10-year average snow free period lasted for 169 ± 42 days (Havranek 1987), which matches the time available for maintaining a positive carbon balance in adult *Pinus cembra* trees (Wieser et al. 2005).

In tropical treeline species by contrast, there is a continuous growing season where night frosts contrast with favourable conditions during the day (Rada et al. 1996). Thus, despite the evident relatedness of tree life limitation at high altitude to temperature, the physiological mechanisms

involved are still under debate and a multitude of factors, acting singly or in combination have been proposed to be responsible for the upper elevational limit of tree life (Wardle 1974, 1993; Tranquillini 1979; Körner 1998, 2003; Holtmeier 2003). Current hypotheses attempting to explain tree life limitation at the climate driven upper timberline include climatic stress, disturbance, an insufficient carbon balance, a limitation to cell growth and tissue formation, limited nutrient supply, as well as limited regeneration.

1.3.1 Climatic stress

According to ideas going back to Michaelis (1934a, b) the success of trees at high elevations depends on the ripening of their shoots, so that they can withstand unfavourable periods, which in temperate regions corresponds to the winter. Ripening can be defined as the completion of growth combined with lignified cell walls and the development of a thick cuticle and thus allowing withstanding low temperatures and freeze dehydration. Physiologically this acquisition is associated with an increase in the osmotic concentration of the cell sap, a decrease of free water in the protoplasm, permeable protoplasts tolerant to considerable dehydration, and no tissue damage due to intercellular ice formation (Levitt 1972).

Winter desiccation or *frost drought* is assumed to be one of the main causes for the upper limit of tree growth in high mountains outside the tropics (Turner 1968; Tranquillini 1976, 1979; Baig and Tranquillini 1980; Schwarz 1983; Christerson et al. 1988) because of insufficient maturation of cuticles and buds during the preceding summer (Holtmeier 1974; Hadley and Smith 1989). Winter desiccation can occur throughout the winter and in early spring when water losses by cuticular transpiration can not be compensated due to frozen soil and above ground tissues (Michaelis 1934a; Larcher 1957, 1963, 1985; Tranquillini 1976, 1979, 1982; Sowell et al. 1982; Sakai and Larcher 1987; Hadley and Smith 1990; Havranek and Tranquillini 1995; Neuner et al. 1999). Winter desiccation injury may also result from unfrozen cold soils (Grier 1988; Kullmann 1996). Wax erosion caused by winter wind abrasion also can influence needle mortality due to excess moisture loss (Hadley and Smith 1987, 1989).

Frost damage may also be a contributing factor to tree life limit at high elevations. Damage due to direct effects of low temperatures however, seems to be less important than winter desiccation (Wardle 1974). Although outside the tropics the frost tolerance of treeline-forming tree species generally exceeds the environmental demand, frequent and rapid freeze thaw cycles (Larcher 1985; Hadley and Smith 1987; Gross et

al.1991; Perkins et al. 1991; Havranek and Tranquillini 1995; Perkins and Adams 1995) as well as light frosts during the growing season may cause severe damage. Freezing sensitivity has also been reported for chilling resistant conifers on oceanic islands in southern Europe (Peters et al. 1999). In the tropics, freezing injury theoretically may occur at any day of the year (Beck et al. 1984; Rada et al. 1985; Goldstein et al. 1994; Rundel 1994).

As a result of cold acclimation, an increased resistance to phototoxic effects (Öquist and Huner 1991) is also beneficial for the survival of hardy plants during the cold season, when high irradiance can occur in combination with low temperature. Such conditions will lead to the formation of reactive oxygen species (Elstner and Oßwald 1994). These molecules are destructive due to their capacity to start radical cascade reactions and must be controlled by protective systems (Demming-Adams et al. 1994; Polle and Rennenberg 1994; Noctor and Foyer 1998). Under such conditions, defence systems are highly activated, probably to the very limit, when compared to trees growing below the timberline (Tausz et al. 1998a, b).

1.3.2 Disturbance

Mechanical damage by wind, ice blasting, snow break, and avalanches affect trees mechanically and physiologically. Windthrow of trees and mechanical damage due to breaking of twigs and branches is a remarkable occurrence in the timberline ecotone (Däniker 1923). Crown forms such as *flagged krummholz* are also sculptured by wind. Mechanical damage due to ice-blasting has also been described (Müller-Stohl 1954; Van Gradingen et al. 1991). On the other hand, microscopic studies were unable to confirm wind induced damage on needle cuticles of *Pinus cembra* caused by snow polishing or whipping of branches in storms (Holzer 1959; Platter 1976).

Wind also increases the boundary layer conductance, affects evapotranspiration and influences the depletion of protective snow (Larcher 1985). Cold winds accelerate the penetration of low temperatures and soil frost in snow-free habitats and rocks (Aulitzky 1961; Bonan 1992), and thus also favouring winter desiccation. Once dry, such shoots then may secondarily be damaged by the mechanical action of the wind.

In temperate timberline ecotones snow distribution by wind is of paramount importance to the site conditions (Holtmeier 2003). Beside destruction by avalanches, a permanent snow cover in temperate mountains affects the length of the growing season. Seedlings and small trees buried below snow however, might be protected from animals and photo-oxidative

stress during the winter. On the other hand, trees under snow lose their frost resistance and can easily be damaged by low temperatures after being released (Tranquillini 1959). Moreover, the high humidity of the air together with a constant temperature of about 0 °C below the snow surface, favours the attack of weakened trees by parasitic snow fungi such as *Heripitrichia* spp. and *Phacidium* spp. (Donaubauer 1963), which can cause widespread damage in winters with an exceptional long snow cover (Aulitzky and Turner 1982).

1.3.3 Insufficient carbon balance

Several authors argued that the upper limit of tree growth might be caused by an insufficient carbon balance due to an unfavourable leaf mass ratio (i.e. the amount of leaf dry matter in % of total tree biomass) when compared to dwarf shrubs and alpine pasture species (Boysen-Jensen 1932; Ellenberg 1975; Stevens and Fox 1991; Slatyer and Noble 1992; Körner 1994; Cairns 1998; Cairns and Malanson 1998).

At the leaf level, the annual carbon uptake is mainly influenced by the length of the growing season and by the supply of solar radiation during daylight hours within a given season length. In mountains outside the tropics season length also affects the annual carbon balance of entire trees due to respiratory losses during the period of winter dormancy. At the alpine timberline in 1950 m a.s.l. in the central Austrian Alps (Klimahaus Research Station near Innsbruck; 47° N, 11° E) the total measured carbon loss during the winter of *Pinus cembra* twigs (22-33 mg CO₂ per g needle dry mass) has been shown to equal the photosynthetic production of one to two warm days in spring or summer, when the average air temperature is above 6 °C (Wieser 1997). For *Pinus aristata* growing at 3100 m altitude in the White Mountains of California, USA, Schulze et al. (1967) calculated a total respiratory loss of 140 mg CO₂ per g needle dry mass in winter which can be recovered within two to three weeks of photosynthesis during the summer.

During the leafless period from October to April, whole tree respiration of *Larix decidua* at the alpine timberline in 1950 m a.s.l. in the central Austrian Alps (Klimahaus Research Station) was calculated to be only 2.3 % of its annual photosynthetic carbon gain (Havranek and Tranquillini 1995). Whole year round above ground woody tissue respiration in adult *Pinus cembra* and *Larix decidua* trees in the timberline ecotone were calculated to be 39 and 17 %, respectively of the annual carbon gain fixed by net photosynthesis (Tranquillini and Schütz 1970; Wieser et al. 2005). In addition in the timberline ecotone carbon loss through root respiration is

remarkably small when compared with trees from lower altitudes (Tranquillini 1979), which can be attributed to a small root to leaf mass ratio and to low soil temperatures.

On the other hand, Kuuluvainen et al. (1996) showed that increasing drought can induce needle loss in *Abies lasiocarpa* seedlings at their upper limit in the Olympic Mountains, Washington, USA in such a way that may result in a negative carbon balance in the longer term.

Recently it has been argued that the upper limit of tree life might be caused by a zero balance between production and all the losses of organic matter, including respiration and dieback of older needles, branches and roots (Körner 2003; Paulsen et al. 2000). Thus, carbon allocation rather than carbon gain might be the critical factor and an increase of heterotrophic versus autotrophic tissue might influence the carbon balance with increasing elevation.

However, in trees similar in age there was no change in dry matter allocation across the treeline ecotone (Oswald 1963), and with increasing altitude even an increase in needle mass per total tree biomass was observed (Bernoulli and Körner 1999). In addition, non-structural carbohydrates and lipid pools within the whole tree biomass tend to increase with elevation within the timberline ecotone (Hoch et al. 2002), and thus suggesting that an increase in carbon storage with increasing elevation rather than a limitation in carbon gain might limit tree life at the timberline (Körner 1998, 2003; Hoch et al. 2002; Hoch and Körner 2003).

1.3.4 Limitation to cell growth and tissue formation

Increased concentrations of total non-structural carbohydrates and lipid pools at the upper limit of tree growth might be due to a low temperature limitation of cell growth and tissue formation (Däniker 1923; Körner 1998, 2003) when small trees emerge. Approaching their upper limit trees become more stunted with shorter stems and more branches (Bernoulli and Körner 1999). Thus apical shoots might not benefit from radiant warming when compared to lateral shoots closer to the warm topsoil (Wieser 2002).

In *Pinus cembra* radial cambium growth during the growing season ceased whenever temperature dropped below approximately 5 °C (Loris 1981; Wieser 2002). In timberline conifers apical shoot height extension and root growth ceases at a threshold temperature between 5 and 7 °C (James et al 1992; Kronfuss 1994; Häsler et al. 1999).

Low root zone temperatures also affect shoot functioning such as photosynthesis, transpiration (Havranek 1972), and leaf conductance (Körner

1994; Wieser 2000) and thus suggest a critical temperature for growth under otherwise favourable above soil conditions during the day.

1.3.5 Nutritional limitation

Tree growth at its upper distribution limit has also been shown to be affected by soil nutrient availability (Steinbjörnsson et al. 1992; Karlsson and Weih 2001). Soil micro-organisms play a key role in regulating the availability of nutrients through mineralization of organic matter and the solubilisation of soil minerals (Lee and Pankhurst 1992; Aerts 2002). Thus, it is appropriate to mention that only trees in symbiosis with ectomycorrhizal fungi are capable of reaching their upper altitudinal limit (Moser 1967). This is further corroborated by the suggestion that the ectomycorrhizal symbiosis made it possible for trees to colonise boreal zones, where there is a low availability of nutrients, mainly nitrogen and phosphorus (Read 1991). In general, mycorrhization tends to decrease with increasing altitude (Read and Haselwandter 1981). Mycorrhizal symbionts are also host dependent (Molina and Trappe 1982) and different tree species may selectively stimulate the growth of different microbial species (Garyston and Campbell 1996). In addition, microbial growth might probably be carbon limited, which in the case of ectomycorrhizal fungi is from the tree's carbohydrates (Olsson et al. 2002) due to rhizodeposition.

Compared to the closed forest below timberline ecotones are characterised by a mosaic of different soil types (Holtmeier 2003) due to differences in microclimate, vegetation cover, and hence also in nutrient sources. Thus, plant-soil feedbacks due to differences in the use of nutrient sources and litter decomposition by different mycorrhiza types (ecto-, ericoid and arbuscular mycorrhizal fungi) might determine competition between timberline tree species, dwarf shrubs, and alpine pasture species, respectively, and thus suggesting a strong below ground control on the upper limit of tree growth.

1.3.6 Limited regeneration

On the long term, beside resistance to the harsh environment, the position of the upper timberline depends also on natural regeneration. Regeneration by seeds depends on a sequence of favourable events (Arno 1984) including the production of good seed crops, suitable seed beds or microsites, and finally on favourable weather conditions during the first growing season. In the timberline ecotone good seed crops occur at intervals of about

3 to 11 years (Rohmeder 1941; Tschermak 1950; Oswald 1963; Franklin et al. 1971). However, the proportion of viable seeds is only very small (Norton and Schönenberger 1984; Sveinbjörnsson et al. 1996). Depending on species, seeds are dispersed into suitable microsites either by winds or by animals.

Invasion of seedlings into meadows and snowdrift sites is another aspect of seed-initiated regeneration (Franklin et al. 1971; Dunwiddie 1977).

Some tree species have developed the ability to spread through layering (Arno 1984) which becomes effective at moist snowy sites (Arno 1984), in zones where the climate does not favour sexual regeneration (Larcher 1980), and where a dense surface vegetation presents a formidable barrier for seedling establishment.

Furthermore, seedling mortality is also an important factor in new seedling establishment in the timberline ecotone (Germino et al. 2003) because abiotic factors can reduce photosynthetic carbon gain (Johnson et al. 2004). In addition, these factors are also associated with decreased root growth and low mycorrhizal infection (Ciu and Smith 1991; Miller et al. 1998). These factors include low minimum night temperatures and suboptimal (too low and too high) sunlight (Cui and Smith 1991; Germino and Smith 1999; Germino et al. 2003). For example, in the Bow Mountains in southern Wyoming, USA photosynthetic carbon gain in young seedlings of *Abies lasiocarpa* and *Picea engelmannii* at treeline (3200 m a.s.l.) was reduced by 19 and 29 %, respectively when compared to an adjacent forest understory (2965 m a.s.l.) and appeared to be primarily associated to more sky exposure and hence also lower minimum night temperatures at the higher- elevation site (Johnson et al. 2004). In addition, at the high elevation site the mortality rate of *Picea engelmannii* seedlings tended to increase with exposure to cold night temperatures and high sunlight during the following day (Germino and Smith 2000).

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