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Trees at their Upper Limit

Treelife Limitation at the Alpine Timberline

Edited by
Gerhard Wieser
and
Michael Tausz

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Edited by

Gerhard Wieser
Federal Research and Training Centre for Forests,
Natural Hazards and Landscape (BFW), Innsbruck, Austria

and

Michael Tausz
The University of Melbourne
Creswick, VIC, Australia

Springer

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Cover illustration: The timberline ecotone in the central Alps south of Innsbruck, Austria with the Stubaier Alpen in the background. (Photo: J. Wagner, Institut für Botanik, Universität Innsbruck.)

Contents

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 researchers, 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.

Gerhard Wieser
Innsbruck, Austria

Michael Tausz
Melbourne, Australia

Contributors

Helmut Bauer
Institut für Botanik, Universität Innsbruck
Sternwartestraße 15, 6020 Innsbruck
Austria

Brigitta Erschbamer
Institut für Botanik, Universität Innsbruck
Sternwartestraße 15, 6020 Innsbruck
Austria

Kurt Haselwandter
Institut für Mikrobiologie, Universität Innsbruck
Technikerstraße 25, 6020 Innsbruck
Austria

Stefan Mayr
Institut für Botanik, Universität Innsbruck
Sternwartestraße 15, 6020 Innsbruck
Austria

Gilbert Neuner
Institut für Botanik, Universität Innsbruck
Sternwartestraße 15, 6020 Innsbruck
Austria

Walter Oberhuber
Institut für Botanik, Universität Innsbruck
Sternwartestraße 15, 6020 Innsbruck
Austria

Christian Schwaninger
Abteilung Waldschutz, Amt der Tiroler Landesregierung
Bürgerstraße 36, 6020 Innsbruck
Austria

Dieter Stöhr
Abteilung Forstorganisation, Amt der Tiroler Landesregierung
Bürgerstraße 36, 6020 Innsbruck
Austria

Michael Tausz
School of Forest and Ecosystem Science, University of Melbourne
Water Street, Creswick, Victoria 3363
Australia

Susanne Wallnöfer
Institut für Botanik, Universität Innsbruck
Sternwartestraße 15, 6020 Innsbruck
Austria

Gerhard Wieser
Institut für Naturgefahren und Waldgrenzregionen, Bundesforschungs- und Ausbildungszentrum für Wald, Naturgefahren und Landschaft (BFW)
Rennweg 1, 6020 Innsbruck
Austria

1 Current Concepts for Treelife Limitation at the Upper Timberline

Gerhard Wieser[1] and Michael Tausz[2]

[1]Institut für Naturgefahren und Waldgrenzregionen, BFW, Innsbruck
[2]School of Forest and Ecosystem Science, University of Melbourne

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,

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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; Piussi and Schneider1985; 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*".

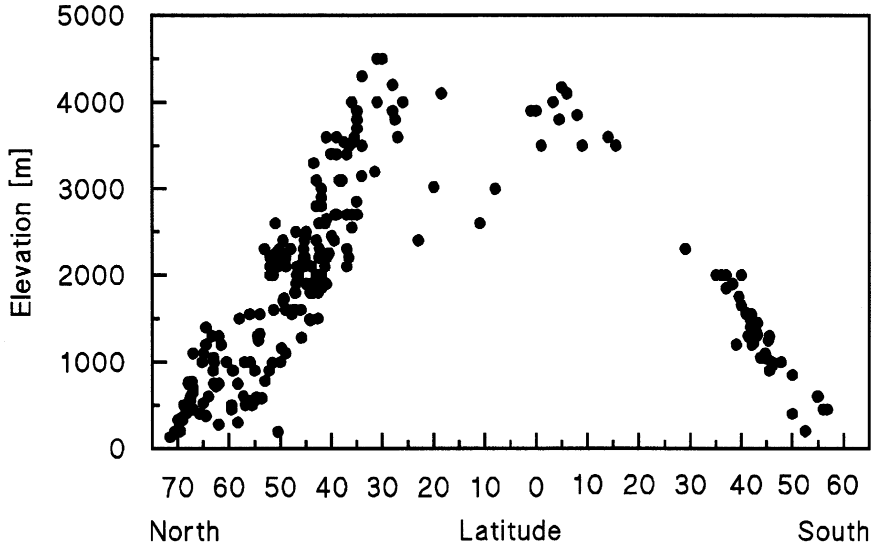

Fig. 1.1. The latitudinal position of the upper the treeline. (Redrawn after data collected by Hermes 1955; Wardle 1974; Franz 1979; Arno 1984; and Jobbagy and Jackson 2000.)

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 my 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, 1779, 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 show-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 CO_2 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 CO_2 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 engelmanii* 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 engelmanii* seedlings tended to increase with exposure to cold night temperatures and high sunlight during the following day (Germino and Smith 2000).

References

Aerts R (2002) The role of various types of mycorrhizal fungi in nutrient cycling and plant competition. In: Van der Heijden MGA, Sanders I (eds) Mycorrhizal ecology. Ecological Studies, vol 157. Springer, Berlin, Heidelberg, New York, pp 117-133

Arno MF (1984) Timberline: mountain and arctic forest frontiers. The Mountaineers, Seattle

Aulitzky H (1961) Die Bodentemperaturverhältnisse in der Kampfzone oberhalb der Waldgrenze und im subalpinen Zirben-Lärchenwald. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 153-208

Aulitzky H, Turner H (1982) Bioklimatische Grundlagen einer standortsgemäßen Bewirtschaftung des subalpinen Lärchen-Arvenwaldes. Mitteilungen Eidgenössische Anstalt für das Forstliche Versuchswesen 58: 327-580

Baig MN, Tranquillini W (1980) The effects of wind and temperature on cuticular transpiration of *Picea abies* and *Pinus cembra* and their significance in desiccation damage at the alpine treeline. Oecologia 47: 252-256

Beck E, Schulze E-D, Senser J, Scheibe R (1984) Equilibrium freezing of leaf water and extracellular ice formation in afroalpine “giant rosette” plants. Planta 162: 276-282

Bernoulli M, Körner Ch (1999) Dry matter allocation in treeline trees. Phyton 39: 7-12

Bonan GB (1992) Soil temperature as an ecological factor in boreal forests. In: Shugart HH, Leemans R, Bonan GB (eds) A system analysis of the global boreal forest. Cambridge University Press, Cambridge, pp 126-143

Boysen-Jensen P (1932) Die Stoffproduktion der Pflanzen. Fischer, Jena

Brockmann-Jerosch H (1919) Baumgrenze und Klimacharakter. Pflanzengeographische Kommission der Schweizerischen Naturforschenden Gesellschaft. Beiträge zur Landesaufnahme 6. Rascher und Cie, Zürich

Cairns DM (1998) Modelling controls on pattern at alpine treeline. Geographical and Environmental Modelling 2: 43-64

Cairns DM, Malanson GP (1998) Environmental variables influencing the carbon balance at the alpine treeline: a model approach. Journal of Vegetation Science 9: 697-692

Christersson L, von Fricks H, Sihe Y (1988) Damage to conifer seedlings by summer frost and winter drought. In: Sakai A, Larcher W (eds) Plant cold hardiness. Alan R Liss, Inc., pp 203-210

Ciu M, Smith WK (1991) Photosynthesis, water relations and mortality in *Abies lasiocarpa* seedlings during natural establishment. Tree Physiology 8: 37-46

Cogbill CF, White PS (1991) The latitude-elevation relationship for spruce-fir forest line along the Appalachian mountain chain. Vegetatio 94: 153-175

Däniker A (1923) Biologische Studien über Baum- und Waldgrenzen, insbesondere über die klimatischen Ursachen und deren Zusammenhänge. Vierteljahres-schrift der Naturforschenden Gesellschaft in Zürich 68: 1-102

Daubenmire R (1954) Alpine treelines in the Americans and their interpretation. Butler University Botanical Studies 2: 119-136

Demmig-Adams B, Adams III WW (1994) Light stress and photoprotection related to the xanthophyll cycle. In: Foyer CH, Mullineaux PM (eds) Causes of photooxidative stress and amelioration of defense systems in plants. CRC Press, Boca Raton, pp 105-126

Donaubauer E (1963) Über die Schneeschütte-Krankheit (*Phacidium infestans* Karst.) der Zirbe (*Pinus cembra* L.) und einiger Begleitpilze. Mitteilungen der Forstlichen Versuchsanstalt Mariabrunn 60: 147-166

Dunwiddie PW (1977) Recent tree invasion of subalpine meadows in the Wind River Mountains, Wyoming. Arctic and Alpine Research 11: 234-251

Ellenberg H (1975) Vegetationsstufen in perhumiden bis perariden Bereichen der tropischen Anden. Phytocoenologia 2: 368-387

Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. Verlag Eugen Ulmer, Stuttgart

Elstner EF, Oßwald W (1994) Mechanisms of oxygen activation during plant stress. Proceedings of the Royal Society of Edinburgh 102b: 131-154

Franklin JF, Moir WH, Douglas GW, Wiberg C (1971) Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arctic and Alpine Research 3: 215-224

Franz H (1979) Ökologie der Hochgebirge. Ulmer, Stuttgart

Friedel H (1967) Verlauf der alpinen Waldgrenze im Rahmen anliegender Gebirgsgelände. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 75: 81-172

Friedland AL, Boyce RL, Webb ET (1992) Winter and early spring microclimate of a subalpine spruce-fir forest canopy in central New Hampshire. Atmospheric Environment 24A: 1361-1369

Garyston SJ, Campbell CD (1996) Functional biodiversity of microbial communities in the rhizosphere of hybrid larch (*Larix eurolepis*) and Sitka spruce (*Picea sitchensis*). Tree Physiology 16: 1031-1038

Germino MJ, Smith WK (1999) Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. Plant, Cell and Environment 22: 407-415

Germino MJ, Smith WK (2000) Differences in microsite, plant form and low-temperature photoinhibition in alpine plants. Arctic, Antarctic, and Alpine Research 30: 388-396

Germino MJ, Smith WK, Resor AC (2003) Conifer seedling distribution and survival in an alpine-treeline ecotone. Plant Ecology 162: 157-168

Goldstein G, Meizner FC, Rada F (1994) Environmental biology of a tropical treeline species, *Polylepis sericea*. In: Rundel PW, Smith AP, Meizner FC (eds) Tropical alpine environments. Cambridge University Press, Cambridge, pp 1269-149

Grace J (1977) Plant response to wind. Academic Press, London

Grier C (1988) Foliage loss due to snow, wind, and winter drying damage: its effects on leaf biomass of some western conifers. Canadian Journal of Forest Research 18: 1097-1102

Gross M (1989) Untersuchungen an Fichten der alpinen Waldgrenze: Dissertationes Botanicae 139. Kramer, Berlin, Stuttgart

Gross M, Rainer I, Tranquillini W (1991) Über die Frostresistenz der Fichte mit besonderer Berücksichtigung der Zahl der Gefrierzyklen und der Geschwindigkeit der Temperaturänderung beim Frieren und Auftauen. Forstwissenschaftliches Centralblatt 110: 207-217

Hadley JL, Smith WK (1987) Influence of krummholz mat microclimate on needle physiology and survival. Oecologia 73: 82-90

Hadley JL, Smith WK (1989) Wind erosion of leaf surface wax in timberline conifers. Arctic and Alpine Research 21: 392-398

Hadley JL, Smith WK (1990) Influence of leaf surface wax and leaf area to water content ratio on cuticular transpiration in western conifers, U.S.A. Canadian Journal of Forest Research 20: 1306-1311

Häsler R, Streule A, Turner H (1999) Shoot and root growth of young *Larix decidua* in contrasting microenvironments near the alpine treeline. Phyton 39: 47-52

Havranek WM (1972) Über die Bedeutung der Bodentemperatur für die Photosynthese und Transpiration junger Forstpflanzen und die Stoffproduktion an der Waldgrenze. Angewandte Botanik 46: 101-116

Havranek WM (1987) Physiologische Reaktionen auf Klimastreß bei Bäumen an der Waldgrenze. GSF Bericht 10: 23-36

Havranek WM, Tranquillini W (1995) Physiological processes during winter dormancy and their ecological significance. In: Smith WK, Hinckley TM (eds) Ecophysiology of coniferous forests. Academic Press, San Diego, pp 95-124

Hermes K (1955) Die Lage der oberen Waldgrenze in den Gebieten der Erde und ihr Abstand zur Schneegrenze. Kölner Geographische Arbeiten 5

Hoch G, Körner Ch (2003) The carbon charging of pines at the climatic treeline: a global comparison. Oecologia: 219-224

Hoch G, Popp M, Körner Ch (2002) Altitudinal increase of mobile carbon pools in *Pinus cembra* suggests sink limitation of growth at the Swiss treeline. Oikos 98: 361-374

Holtmeier FK (1974) Geoökologische Beobachtungen und Studien an der subarktischen und alpinen Waldgrenze in vergleichender Sicht. Steiner, Wiesbaden

Holtmeier FK (1993) The upper timberline: ecological and geographical aspects. In: Anfodillo T, Urbinati C (eds) Ecologia delle foreste di alta quota. Pubblicazioni del Corso di Cultura in Ecologia 30, pp 1-26

Holtmeier F-K (2003) Mountain timberlines. Ecology, patchiness, and dynamics. Advances in Global Change Research, vol 14. Kluwer Academic Publishers, Dordrecht, Boston, London

Holzer K (1959) Winterliche Schäden an Zirben nahe der alpinen Baumgrenze. Centralblatt für das Gesamte Forstwesen 76: 232-244

James JC, Grace J, Hoad SP (1992) Growth and photosynthesis of *Pinus sylvestris* at its altitudinal limit in Scotland. Journal of Ecology 82: 297-306

Jobbagy EG, Jackson RB (2000) Global controls of forest line elevations in the northern and southern hemispheres. Global Ecology and Biogeography 9: 253-268

Johnson DM, Germino MJ, Smith WK (2004) Abiotic factors limiting photosynthesis in *Abies lasiocarpa* and *Picea engelmannii* seedlings below and above the alpine timberline. Tree Physiology 24: 377-386

Jordan DN, Smith WK (1994) Energy balance analysis of night-time leaf temperatures and frost formation in a subalpine environment. Agricultural and Forest Meteorology 71: 359-372

Karlsson PS, Weih M (2001) Soil temperature near the distribution limit of mountain birch (*Betula pubescens* ssp. *czerepanovii*): implications for seedling nitrogen economy and survival. Arctic, Antarctic, and Alpine Research 33: 88-92

Körner Ch (1994) Leaf conductance in the major vegetation types of the globe. In: Schulze E-D, Caldwell MM (eds) Ecophysiology of photosynthesis. Ecological Studies, vol 100. Springer, Berlin, Heidelberg, New York, pp 463-490

Körner Ch (1998) A re-assessment of high elevation treeline positions and their explanation. Oecologia 115: 445-459

Körner Ch (2003) Alpine plant life: functional plant ecology of high mountain ecosystems, 2nd edn. Springer, Berlin

Körner Ch, Paulsen J (2004). A world-wide study of high altitude treeline temperatures. Journal of Biogeography 31: 713-732.

Kronfuss H (1994) Der Einfluß der Lufttemperatur auf das Höhenwachstum der Zirbe. Centralblatt für das Gesamte Forstwesen 11: 165-181

Kullmann L (1996) Rise and demise of cold-climate *Picea abies* forest in Sweden. New Phytologist 134: 243-256

Kuuluvainen T, Sprugel DG, Brooks JR (1996) Hydraulic architecture and structure of *Abies lasiocarpa* seedlings in three subalpine meadows of different moisture status a in the Eastern Olympic Mountains, Washington. Arctic and Alpine Research 28: 60-64

Larcher W (1957) Frosttrocknis an der Waldgrenze und in der alpinen Zwergstrauchheide. Veröffentlichungen Museum Ferdinandeum, Innsbruck 37: 49-81

Larcher W (1963) Zur spätwinterlichen Erschwerung der Wasserbilanz von Holzpflanzen an der Waldgrenze. Berichte des Naturwissenschaftlich Medizinischen Vereins in Innsbruck 53: 125-137

Larcher W (1980) Klimastreß im Gebirge – Adaptationstraining und Selektionsfilter für Pflanzen. Rheinisch-Westfälische Akademie der Wissenschaften, Vorträge 291: 49-88

Larcher W (1985) Winter stress in high mountains. In: Turner H, Tranquillini W (eds) Establishment and tending of subalpine forests: research and management. Berichte Eidgenössische Anstalt für das Forstliche Versuchswesen 270, pp 11-20

Lee KE, Pankhurst CE (1992) Soil organisms and sustainable productivity. Australian Journal of Soil Research 30: 855-892

Levitt J (1972) Response of plants to environmental stresses. Academic Press, New York, London

Loris K (19819 Dickenwachstum von Zirbe, Fichte und Lärche an der alpinen Waldgrenze/Patscherkofel. Ergebnisse der Dendrometermessungen 1976-79. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 142: 416-441

Michealis P (1934a) Ökologische Studien an der Baumgrenze, IV. Zur Kenntnis des winterlichen Wasserhaushaltes. Jahrbuch für wissenschaftliche Botanik 80: 169-247

Michealis P (1934b) Ökologische Studien an der Baumgrenze, V. Osmotischer Wert und Wassergehalt während des Winters in den verschiedenen Höhenlagen. Jahrbuch für wissenschaftliche Botanik 80: 337-362

Miller SL, McLean TM, Stanton NL, Williams SE. (1998) Survivability, physiognomy and mycorrhization of first year conifer seedlings following fire in Grand Teton National Park. Canadian Journal of Forest Research 28: 115-122

Molina R, Trappe JM (1982) Patterns of ectomycorrhizal host specificity and potential among Pacific Nortwest conifers and fungi. Forest Science 28: 423-458

Moser M (1967) Die ektotrophe Ernährungsweise an der Waldgrenze. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 75: 357-380

Müller-Stohl WR (1954) Beiträge zur Ökologie der Waldgrenze am Feldberg im Schwarzwald. In: Janchen E (ed) Angewandte Pflanzensoziologie, Festschrift Erwin Aichinger, vol 2. Springer, Wien, pp 824-847

Neuner G, Ambach, D, Buchner O (1999) Readiness to frost harden during the dehardening period measured in situ in leaves of *Rhododendron ferrugineum* L. at the alpine timberline. Flora 194: 289-296

Noctor G, Foyer CH (1998) Ascorbate and glutathione. Keeping active oxygen under control. Annual Review of Plant Physiology and Plant Molecular Biology 49: 249-279

Norton DA, Schönenberger W (1984) The growth forms and ecology of *Nothofagus solandri* at the alpine timberline, Craigieburn Range, New Zealand. Arctic and Alpine Research 16: 361-370

Olsson PA, Jakobsen I, Wallander H (2002) Foraging and resource allocation strategies of mycorrhizal fungi in a patchy environment. In: Van der Heijden MGA, Sanders I (eds) Mycorrhizal ecology. Ecological Studies, vol 157. Springer, Berlin, Heidelberg, New York, pp 937-115

Öquist G, Huner NPA (1991) Effect of cold acclimation on the susceptibility of photosynthesis to photoinhibition in Scots pine and in winter and spring cereals: a fluorescence analysis. Functional Ecology 5: 91-100

Oswald H (1963) Verteilung und Zuwachs der Zirbe (*Pinus cembra* L.) der subalpinen Stufe an einem zentralalpinen Standort. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 60: 439-499

Paulsen J, Weber UM, Körner Ch (2000) Tree growth near treeline: abrupt or gradual reduction with altitude. Arctic, Antarctic, and Alpine Research 32: 14-20

Perkins TD, Adams GT (1995) Rapid freezing induces winter injury symptomatology in red spruce foliage. Tree Physiology 15: 259-266

Perkins TD, Adams GT, Klein RM (1991) Desiccation or freezing? Mechanisms of winter injury to red spruce foliage. American Journal of Botany 78: 1207-1217

Peters J, Jimenez MS, Morales D (1999) Effect of extreme temperatures on the photosynthetic apparatus of the canarian endemic pine (*Pinus canariensis*). Zeitschrift für Naturforschung 54: 681-687

Piussi P, Schneider A (1985) Die obere Wald- und Baumgrenze im Pfitschtal (Südtitol). Centralblatt für das gesamte Forstwesen 102: 234-246

Platter W (1976) Wasserhaushalt, cuticuläres Transpirationsvermögen und Dicke der Cutinschichten einiger Nadelholzarten in verschiedenen Höhenlagen und nach experimenteller Verkürzung der Vegetationsperiode. Ph.D. thesis, Innsbruck University

Polle A, Rennenberg H (1994) Photooxidative stress in trees. In: Foyer CH, Mullineaux PM (eds) Causes of photooxidative stress and amelioration of defence systems in plants. CRC Press, Boca Raton, pp 199-218

Rada F, Goldstein G, Azocar A, Meizner F (1985) Daily and seasonal osmotic changes in a tropical treeline species. Journal of Experimental Botany 36: 989-1000

Rada F, Azocar A, Briceno B, Gonzalez J, Garcia-Nunez C (1996) Carbon and water balance in *Polylepis sericera*, a tropical treeline species. Trees 10: 218-222

Read DJ (1991) Mycorrhizas in ecosystems. Experientia 47: 376-391

Read DJ, Haselwandter K (1981) Observations on the mycorrhizal status of some alpine plant communities. New Phytologist 88: 341-352

Rohmeder E (1941) Die Zirbelkiefer (*Pinus cembra*) als Hochgebirgsbaum. Jahrbuch zum Schutze der Alpenpflanzen und Tiere 13: 27-39

Rundel PW (1994) Tropical alpine climates. In: Rundel PW, Smith AP, Meizner FC (eds) Tropical alpine environments. Cambridge University Press, Cambridge, pp 21-44

Sakai A, Larcher W (1987) Frost survival of plants. Responses and adaptations to freezing stress. Ecological Studies, vol 62. Springer, Berlin, Heidelberg, New York

Schulze E-D, Mooney HA, Dunn EL (1967) Wintertime photosynthesis of bristelcone pine (*Pinus aristata*) in the White Mountains of California. Ecology 48: 1044-1047

Schwarz R (1983) Simulationsstudien zur Theorie der oberen Waldgrenze. Erdkunde 37: 1-11

Scuderi LA (1987) Late-Holocene upper timberline vegetation in the Southern Sierra Nevada, California, USA. Nature 325: 242-244

Slatyer RO, Noble IR (1992) Dynamics of treelines. In: Hansen A, DiCastri F (eds) Landscape boundaries: consequences for biotic diversity and ecological flows. Ecological Studies, vol 92. Springer, Berlin, Heidelberg, New York, pp 346-359

Sowell JB, Kouitnik DL, Lansing AJ (1982) Cuticular transpiration of whitebark pine (*Pinus albicaulis*) within a Sierra Nevadan timberline ecotone, USA. Arctic and Alpine Research 14: 97-103

Stevens GC, Fox JF (1991) The cause of treeline. Annual Review of Ecology and Systematics 22: 177-191

Steinbjörnsson B, Nordell O, Kauhanen H (1992) Nutrient relations of mountain birch growth at and below the elevational tree-line in Swedish Lapland. Functional Ecology 6: 213-220

Stirmbeck GR, Johnsdon AH, Vann DR (1993) Midwinter needle temperature and winter injury on montane red spruce. Tree Physiology 13: 131-144

Sveinbjörnsson B, Kauhanen H, Nordell O (1996) Treeline ecology of mountain birch in the Torneträsk area. Ecological Bulletins 45: 65-70

Tausz M, Jiménez MS, Grill D (1998a) Antioxidative defence and photoprotection in pine needles under field conditions – a multivariate approach to evaluate patterns of physiological responses at natural sites. Physiologia Plantarum 104: 760-764

Tausz M, Stabentheiner E, Wonisch A, Grill D (1998b) Classification of biochemical response patterns for the assessment of environmental stress to

Norway spruce. Environmental Science and Pollution Research, Special Issue No 1: 96-100

Tranquillini W (1959) Die Stoffproduktion der Zirbe an der Waldgrenze während eines Jahres. 1. Standortsklima und CO_2-Assimilation. Planta 54: 107-129

Tranquillini W (1976) Water relations and alpine timberline. In: Lange OL, Kappen L, Schulze E-D (eds) Water and plant life. Ecological Studies, vol 19. Springer, Springer Berlin, Heidelberg, New York, pp 473-491

Tranquillini W (1979) Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. Ecological Studies, vol 31. Springer, Berlin, Heidelberg, New York

Tranquillini W (1982) Frost drought and its ecological significance. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopaedia of plant physiology 12B. Physiological plant ecology II. Springer, Berlin, Heidelberg, New York, pp 379-400

Tranquillini W, Turner H (1961) Untersuchungen über die Pflanzentemperaturen in der subalpinen Stufe mit besonderer Berücksichtigung der Nadeltemperatur der Zirbe. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 127-151

Tranquillini W, Schütz W (1970) Über die Rindenatmung einiger Bäume an der Waldgrenze. Centralblatt für das Gesamte Forstwesen 87: 42-60

Troll C (1973) The upper timberlines in different climatic zones. Arctic and Alpine Research 5: A3-A18

Tschermak L (1950) Waldbau auf pflanzengeographisch-ökologischer Grundlage. Springer, Wien

Turner H (1961) Standortsuntersuchungen in der subalpinen Stufe: Die Niederschlags- und Schneeverhältnisse. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 265-315

Turner H (1968) Über "Schneeschliff" in den Alpen. Wetter und Leben 20: 192-200

Van Gradingen P, Grace J, Jeffree CE (1991) Abrasive damage by wind to the needle surface of *Pinus sylvestris* L. and *Picea sitchensis* (Bong.) Carr. Plant, Cell and Environment 14: 185-193

Wardle P (1974) Alpine timberlines. In: Ives JD, Barry R (eds) Arctic and alpine environments. Methuen Publishing, London, pp 371-402.

Wardle P (1981) Winter desiccation of conifer needles simulated by artificial freezing. Arctic and Alpine Research 13: 419-423

Wardle P (1993) Causes of alpine timberline: a review. In: Alden J (ed) Forest development in cold climates. Plenum Press, pp 89-103

Wieser G (1997) Carbon dioxide gas exchange of cembran pine (*Pinus cembra*) at the alpine timberline during winter. Tree Physiology 17: 473-477

Wieser G (2000) Seasonal Variation of leaf conductance in a subalpine *Pinus cembra* during the winter months. Phyton 40: 185-190

Wieser G (2002) The role of sapwood temperature variations within *Pinus cembra* on calculated stem respiration: implications for upscaling and predicted global warming. Phyton 42: 1-11

Wieser G, Gigele T, Pausch H (2005) The carbon budget of an adult *Pinus cembra* tree at the alpine timberline in the Central Austrian Alps. European Journal of Forest Research 124: 1-8

Zotov VD (1938) Some correlations between vegetation and climate in New Zealand. New Zealand Journal of Science and Technology 19: 474-487

2 Climate at the Upper Timberline

Gerhard Wieser

Institut für Naturgefahren und Waldgrenzregionen, BFW, Innsbruck

2.1 Introduction

Climate[1] is an important factor for tree growth. It governs the stand structure, the species composition, the amount of biomass production, and also sets limits for their survival. Timberline environments are generally characterized by harsh climatic conditions and in general, the existence of the upper timberline is primarily related to heat deficiency (Holtmeier 2003) determining the length of the growing season. Air and soil temperatures during the growing season, radiation, and the duration of the snow cover affect growth, maturation, and metabolic functions of trees (Tranquillini 1979).

However, we cannot discuss about a climate representative for the timberline ecotone in the European Alps, because in addition to altitude the local topography strongly plays a major role in determining the microclimate[2] at any site within the timberline ecotone. Thus, we have to discriminate between effects of altitude and effects of relief. In the timberline ecotone the effect of slope angle and aspect on solar radiation, wind velocity and direction is by far more important than in the closed forest below. Climatic conditions at or near the ground surface are of special importance in the timberline environment since they largely determine the distribution of tree species and other low stature vegetation types within the timberline ecotone (Aulitzky 1963, 1984).

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[1] The meteorological conditions, including temperature, precipitation, and wind, that characteristically prevail in a particular region

[2] The physical state of the atmosphere close to a small surface in relation to plants

G. Wieser and M. Tausz (eds.), Trees at their Upper Limit, 19–36.

2.2 Effects of altitude

Characteristic climatic data over the altitudinal range of tree growth in the central European Alps are summarized in Table 2.1. Further information on mountain climate and microclimate within the timberline ecotone in the European Alps can be found in texts by Schröter (1926), Steinhauser et al. (1960), Ellenberg (1996), Pruzer (1965), Turner (1970), Fliri (1975), Franz (1979), Larcher (2001), Barry (1992), Kuhn (1997), Veit (2002), and Körner (2003).

Table 2.1. Climatic conditions in the Central European Alps at 500 and 2000 m above sea level. (Compiled after data from Schröter 1926; Steinhauser et al. 1960; Ellenberg 1996, Franz 1979; Baumgartner 1980; Fliri 1975; and Veit 2002.)

Height above sea level		500 m	2000 m
Air pressure	[hPa]	995	795
Saturation water vapour pressure	[hPa]	13.9	7.1
Average wind velocity	[m s^{-1}]	1.3	4.0
Solar radiation	[%]	100	114
UV-radiation	[%]	100	124
Average air temperature	[°C]	9.7	2.0
Annual number of frost days		107	202
Annual number of ice days		19	87
Annual number of freeze-thaw days		88	75
Annual precipitation	[mm]	850	1850
Days with snow fall		30	115
Days with snow cover		70	215
Soil temperature 10 cm	[°C]	9.1	3.5

Frost days: minimum daily air temperature < 0 °C; ice days: maximum daily air temperature < 0 °C; freeze-thaw days: difference between frost and ice days

Atmospheric pressure declines almost linearly with increasing altitude. Thus, within the timberline ecotone the air pressure is approximately 20 to 25% lower than at sea level (1013 hPa). In parallel, the partial pressures of its component gases, including N_2, O_2, and CO_2, decreases in the same proportion. Saturation water vapour pressure by contrast, decreases more rapidly with altitude because of condensation as air temperature falls (Table 2.1).

Wind velocity is also generally higher at timberline as compared to lower elevation sites (Table 2.1). It must be noted however, that wind velocity and direction above the forest limit are strongly influenced by large and small scale topography (Barry 1979; see below).

Solar radiation increases by about 10 % per 1000 m from the sea level up to 3000 m because the atmospheric turbidity declines with increasing altitude (Baumgartner 1981). For the same reason diffuse radiation decreases by about 18 % under clear sky but increases by more than 40 % per 1000 m at overcast conditions (Sauberer and Dirmhirn 1958; Dirmhirn 1964; Barry 1992). At average the central ranges of the European Alps experience approximately 10 % more irradiance than the southern and northern outer mountain ranges (Fliri 1975). This is because in the central ranges it is less cloudy (Fliri 1975) and hence the inner ranges also receive less precipitation than the outer rims (Fliri 1975; Frei and Schär 1998; Schmidli et al. 2002; see also Fig. 2.1).

The increase in altitude is also associated with a temperature lapse rate in the free atmosphere of approximately 0.65 K[3] per 100 m of altitude. In the European Alps the reduction in air temperature with altitude varies between 0.35 and 0.7 K per 100 m of altitude during the summer and the winter, respectively, and an annual lapse rate of 0.55 K per 100 m seems to be the best estimate for the European Alps (Franz 1979 and further references therein; Baumgartner 1981). However, extremes of up to 1 K per 100 m and even negative lapse rates may occur during conditions of stormy weather and periods of temperature inversions, respectively.

The general temperature reduction with altitude also results in an increase in frost (minimum daily air temperature < 0 °C) and ice days (maximum daily air temperature < 0 °C) as well as in the number of days with freeze-thaw cycles (i.e. the difference between frost and ice days in terms of Fliri (1975); Table 2.1).

The number of days with frost however, is not related to the length of the vegetation period as there is the possibility of frost every the month throughout a year (Table 2.2). Calculations of the length of the vegetative growth period is often an approximation based on the number of days with mean air temperatures > 10 °C at particular climate stations. Thus, in the timberline ecotone the "*climatic vegetation period*" lasts for approximately 145 days (Friedel 1967; Havranek and Tranquillini 1995).

More precise information about the duration of the actual growth period can be obtained from tree phenological and physiological measurements. The "*potential vegetation period*" for evergreen trees is the snow free period when warmer temperatures are uninterrupted (daily means > 0 °C; cf. Svoboda 1977; Larcher and Wagner 2004). Within the timberline ecotone of the European Alps at 2000 m above sea level the snow free period last for about 140 to 190 days (Schröter 1926; Havranek and Tranquillini 1995;

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[3] According to the International System of Units "Kelvin" (K) is used to show temperature differences

Kronfuss and Havranek 1999; Wieser 2004). In the central European Alps the snow free period is at an average 80 days longer and hence also significantly warmer than in the outer mountain ranges (Ellenberg 1996; Fliri 1975; Holtmeier 2003). These favourable conditions cause the timberline to rise for about 400 m higher in the central Alps as compared to the outer ranges (Brockmann-Jerosch 1919; Schröter 1926; Ellenberg 1996; Grabherr 1997; cf. also Fig. 2.1). Table 2.2 shows the seasonal changes in the thermal conditions at the upper timberline in the Central Austrian Alps.

Table 2.2. Absolute maximum (Abs max), average maximum (Avg max), average (Avg), average minimum (Avg min), and absolute minimum (Abs min) monthly and annual air temperature as well as the number of frost and ice days at the upper timberline on Mt Patscherkofel, Klimahaus Research Station, 1950 m above sea level, Innsbruck, Austria. Observation period: 1963 -2004 (Wieser unpublished). Frost days: minimum daily air temperature < 0 °C; ice days: maximum daily air temperature < 0 °C.

	Abs max °C	Avg max °C	Avg °C	Avg min °C	Abs min °C	Frost days	Ice days
Jan	11.8	5.9	-4.4	-15.5	-28.0	29	18
Feb	14.4	6.6	-4.5	-14.9	-22.4	27	16
Mar	16.0	8.5	-2.5	-14.5	-19.6	26	13
Apr	15.9	10.7	-0.5	-10.4	-18.0	23	9
May	23.0	16.7	4.8	-4.7	-11.9	11	2
Jun	25.1	20.2	7.8	-1.3	-4.8	4	0
Jul	26.0	21.2	10.0	1.1	-5.2	1	0
Aug	25.8	21.6	10.0	1.0	-4.9	1	0
Sep	22.9	17.8	7.1	-1.7	-5.2	4	0
Oct	21.2	14.9	4.1	-6.1	-14.8	11	3
Nov	15.0	10.9	-0.7	-11.5	-22.4	21	10
Dec	13.5	7.8	-3.1	-14.6	-22.9	28	16
Year	26.0	13.4	2.3	-7.7	-28.0	186	87

Although in the European Alps the annual sum of precipitation in general increases with altitude (Table 2.1) there is no unique relation between altitude and precipitation. The annual sum of precipitation increases between a maximum of 200 mm per 100 m of altitude and less than 60 mm per 100 m of altitude in the outer rims and the inner Alpine sectors, respectively (Turner 1961; Fliri 1975; Lauscher 1976). Figure 2.1 clearly shows that on a mesoscale the distribution of precipitation is mainly governed by the topographic slopes at the southern and northern rim which are responsible for atmospheric ascent, enhanced precipitation, and associated rainshadowing in the inner-Alpine areas (Fliri 1975; Frei and Schär 1998; Schmidli et al. 2002).

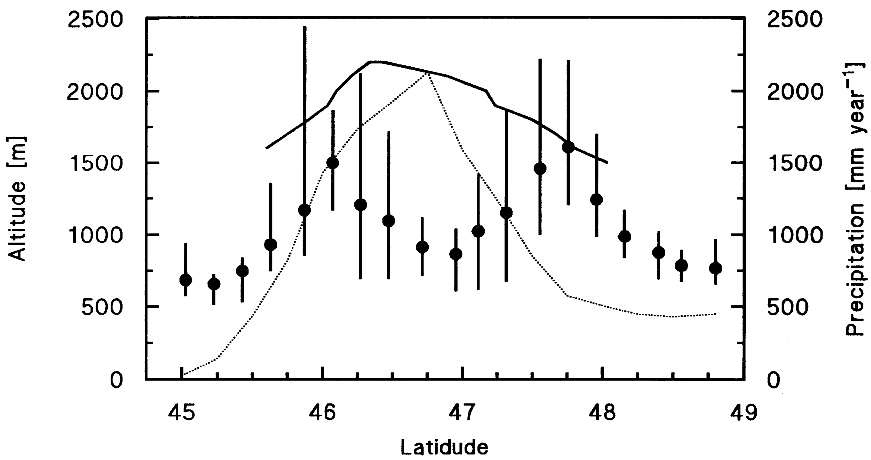

Fig. 2.1. Cross section of average topographic height (dotted line), treeline altitude (solid line), and mean annual precipitation (solid symbols) along a south- north-transect across the eastern Alps. Vertical bars represent the minima and maxima distribution of the mean annual precipitation. (Compiled after data from Brockmann-Jerosch 1919; Schröter 1926; Frei und Schär 1998; and Veit 2002.)

In general, summer is the main rainy season in the Alps and rain or snowfall is observed every third or fourth day on average (cf. Frei and Schär 1998). As a consequence, soils remain continually moist throughout the growing season, and within the timberline ecotone soil moisture seldom drops to values below 20 % by volume (i.e. soil water potentials greater than -0.1 MPa; Neuwinger-Raschendorfer 1961; Neuwinger 1970, 1980; Gunsch 1972; Markart 2000; Wieser 2004).

Due to the decrease in temperature with increasing altitude, there is also a general increase in the number of days with solid precipitation in the form of snow (Table 2.1). Consequently, the annual sum of snow depth also increases with altitude (Fliri 1992; Beniston 1997). Above the forest limit however, snow depth and hence also the duration of the snow cover strongly depends on local topography and on micro-relief (Fiedel 1961; Turner 1961; Kronfuss 1967, 1997; cf. also Fig. 2.2).

2.3 Effects of topography

Since atmospheric conditions become more extreme with increasing altitude (Table 2.1) horizontal climatic differences due to slope angle and relief also tend to increase with increasing altitude. In the timberline ecotone above the forest limit the absence of an ameliorating closed forest canopy results in an amplification of fundamental atmospheric processes in interaction with local site conditions (Figure 2.2). Furthermore, microclimatic conditions are also strongly influenced by scattered stands of trees, an aspect that has hardly been considered in timberline literature so far (Holtmeier 2003).

Slope angle and aspect are the key determinants of topo- and microclimatic differences (Geiger 1961). Differences in radiation doses resulting from topographic features are reflected in variations in soil- and air temperature, snow cover duration, soil moisture, and consequently in the distribution of the vegetation (Aulitzky 1963; Kronfuss 1970; Kronfuss and Stern 1978; Barry and Van Wie 1974; Turner et al. 1975; Larcher 1985; Turner 1993; Fig. 2.2).

The effect of slope angle on the interception of solar radiation is clearly reflected by differences in soil temperature (Fig. 2.2). For example, in one extreme situation at the upper timberline in Obergurgl, Ötztal at 2070 m above sea level Turner (1958a) reported a maximum soil surface temperature of 80 °C on black raw humus on a southwest slope compared with one of only 23 °C on a north-west slope nearby.

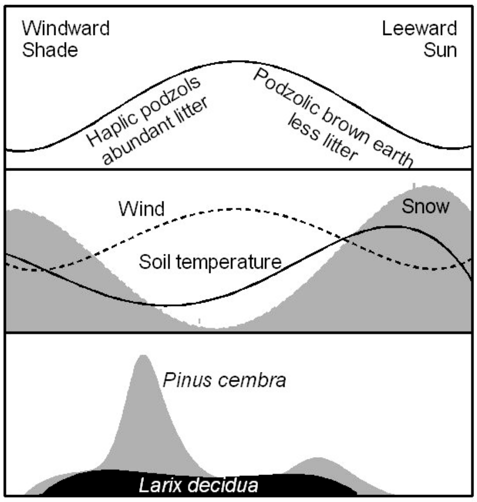

Fig. 2.2. The influence of topography on climatic factors and their effects on soil development and the distribution of conifer seedlings in the timberline ecotone of the Central Austrian Alps. (Modified after Aulitzky 1963, 1984.)

Beside irradiance, wind is another parameter strongly influenced by large-scale and small-scale topography. In the Alps air flow across the mountains give rise to "*Föhn-type*" conditions on leeward slopes (Baumgartner 1980; Fliri 1975; Franz 1979; Vogt 2002). In addition, ridges and gullies within a relief of approximately 10 m can modify the wind velocity by ± 60 % (Aulitzky 1963; Nägeli 1971). Wind also influences the distribution of precipitation, in particular snow (Turner 1961; Kronfuss 1967; Caldwell 1970; Fig. 2.2). Snow tends to be blown off locally from high terrain and thus supporting early season tree growth. On the other hand, greater amounts of snow tend to accumulate in depressions and lee zones.

In addition, small groups of trees significantly reduce the velocity of wind and raise the wind field in the timberline ecotone, where without trees high wind velocities may already occur close to the ground (Aulitzky 1961a; Fig. 2.3).

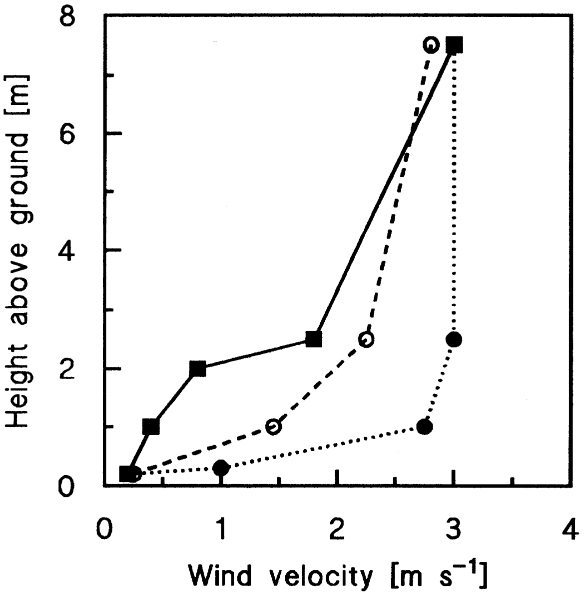

Fig. 2.3. Vertical profiles of wind velocity in the timberline ecotone within a group of *Pinus cembra* trees of about 2 m in height (solid squares and solid line), over treeless areas above the forest limit (open circles and dashed line), and at the tree limit (closed circles and dotted line). Measurements were made in the timberline ecotone at Obergurgl, Austria between 2075 and 2225 m a.s.l. (After Aulitzky 1961a.)

2.4 Canopy and soil temperatures

In addition to topographic effects, plant architecture also strongly determines the microclimate plants experience. Given their life form trees at timberline generally experience a cooler climate as compared to nearby low stature vegetation. This can be related to aerodynamic features (Hadley and Smith 1987; Grace et al. 1989; Körner 2003). The canopy of trees at timberline is aerodynamically rougher than that made of small plants and thus heat dissipation by turbulent convection is higher in the tree's canopy.

Figure 2.4 provides an example of the annual course of air temperature and various tissue temperatures in an adult *Pinus cembra* tree at timberline in the Central Austrian Alps at 1950 m above sea level. In general, needle, apical meristem and above ground cambium temperatures follow the day-by-day variation in air temperature (Fig. 2.4). In spite of the fact that in conifers enlarging buds at the beginning of the growing season as well as the extending shoots are larger than the needles, meristems display higher temperatures than the needles (Grace et al. 1989; Fig. 2.4).

Furthermore, the seasonal and 24-h tissue temperature amplitudes are greater in the upper than in the lower canopy (Fig. 2.4), as also observed in a subalpine spruce-fir forest in central New Hampshire by Friedland et al. (1992). These lower temperature amplitudes in branches and the stem may result from less exposure to direct sunlight due to self shading by outer and upper canopy sections (Wieser 2002).

As a consequence, coarse roots at the soil surface also experience lower temperature amplitudes and temperatures vary between -5 and 25 °C during the winter months and the growing season, respectively (Wieser and Bahn 2004) as compared to above ground woody tissue temperatures, which vary between absolute extremes of -21 and +41 °C (Loris 1981; Gross 1989; Wieser 1997, 2002; Loris et al. 1999; Wieser and Bahn 2004; Fig. 2.4).

In conifers within the timberline ecotone mean leaf to air temperature differences did usually not exceed 0 to 4 K (Turner 1958b; Tranquillini and Turner 1961; Tranquillini 1964; Loris 1981; Hadley and Smith 1987; Gross 1989; Friedland et al. 1992; Wieser 1997, 2002; Loris et al. 1999; Wieser and Bahn 2004). However, depending on branch architecture and wind velocity periods may occur where daytime needle temperature in the fully sunlit upper part of the canopy of *Pinus cembra* trees can be up to 21.5 K warmer than air temperature, and due to radiative cooling night-time needle temperature can be up to 9.3 K less than air temperature (Tranquillini and Turner 1961; Tranquillini 1964; Baig and Tranquillini

1980; Wieser unpublished). For *Picea abies* needles Gross (1989) reports a maximum overheating of +23.5 K and a maximum undercooling of –11 K during the growing season and the winter, respectively (Fig. 2.5).

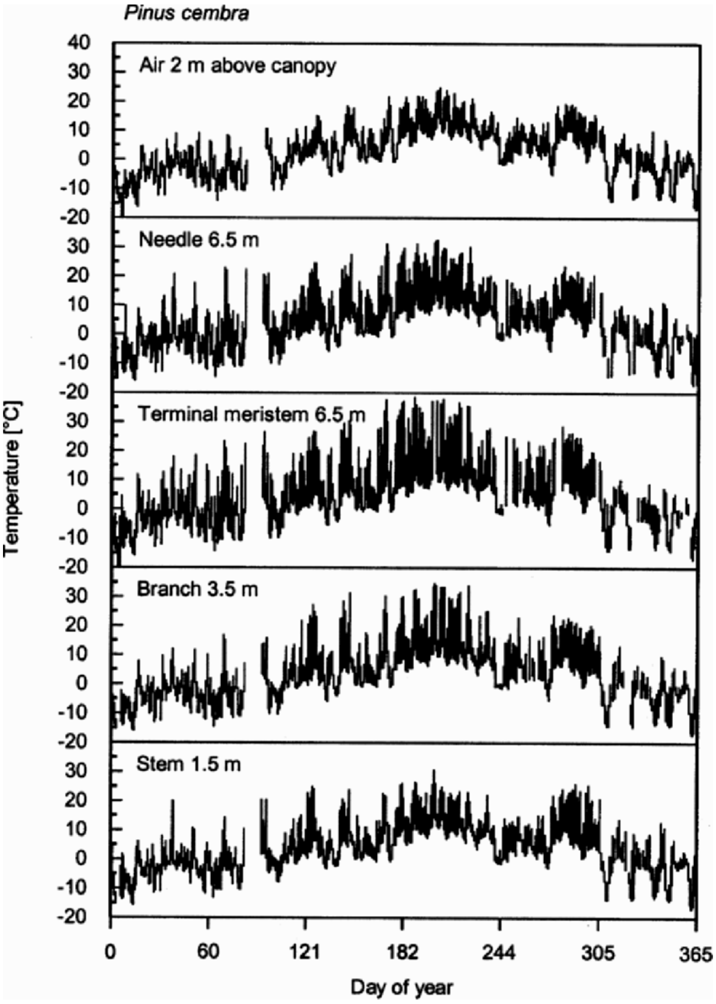

Fig. 2.4. Time course of the amplitude between daily minimum and daily maximum air, needle, terminal meristem, branch, and stem cambium temperature in an adult *Pinus cembra* tree. Measurements were made at Mt. Patscherkofel (Klimahaus), Austria, 1950 m a.s.l. (Modified after data from Wieser 2002 and Wieser unpublished.)

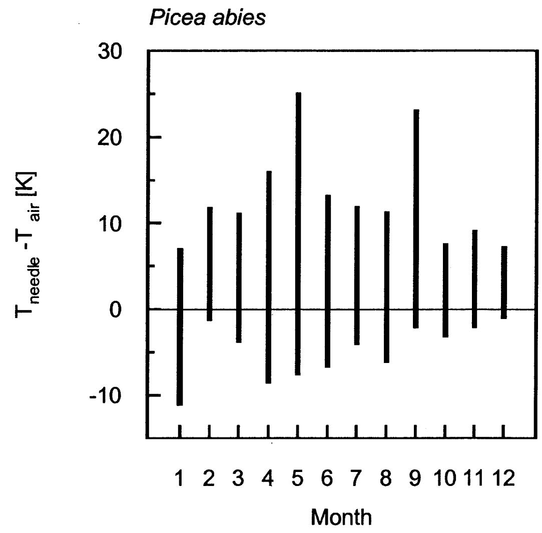

Fig. 2.5. Monthly maximum difference between needle and air temperature in an adult *Picea abies* tree. Measurements were made at Mt. Patscherkofel (Klimahaus), Austria, 1950 m a.s.l. (Modified after Gross 1989.)

Surprisingly, slope exposure (Tranquillini and Turner 1961) and crown position within an entire tree (Gross 1989; Wieser 1997) have no major effects needle temperature. For young *Pinus cembra* trees at the upper timberline in Obergurgl, Ötztal at 2050 m above sea level Tranquillini and Turner (1961) report mean daily growing season needle temperatures between 9.6 and 10.6 °C on a north-west slope as compared to values between 8.2 and 11.7 °C on a south-west slope. Absolute maxima and minima between both sides differed by less than 2 and 1 K, respectively.

When documenting the annual course of needle temperature on south-, west- and east-facing twigs of an adult *Picea abies* at timberline on Mt. Patscherkofel (Klimahaus), Innsbruck at 1950 m above sea level, Gross (1989) failed to find significant differences with respect to compass direction: compared to an annual mean needle temperature of +5.0 °C on south-facing twigs, the corresponding values for west- and east-facing twigs differed by only -0.8 and -0.2 K, respectively. Similar within tree variations in needle temperature were also observed for *Pinus cembra* by Wieser (1997) at the same study site. This is, because within entire tree crowns twigs, and needles create their own interaction angles with solar radiation irrespective from slope direction and crown position.

The mean daily and seasonal temperature difference between above ground woody tissues and the surrounding air is approximately zero (Wieser 2002; Wieser et al. 2005) and – compared to needle temperature - maximum overheating and undercooling are significantly smaller as shown for an entire stem of a *Pinus cembra* tree at timberline on Mt. Patscherkofel (Klimahaus), Innsbruck at 1950 m above sea level in Fig. 2.6.

The higher temperature difference between the south facing stem and the air at the tree trunk results from the exposure to direct sunlight and may also be related to the large heat capacity of woody tissues. Stem temperature at the north side by contrast, is more comparable with air temperature. The lower temperature difference and lower seasonal temperature amplitude between the south-facing stem and the air 4 and 7 m above ground (Fig. 2.6) results from less exposure to direct solar radiation due to self shading by outer branches and twigs, a higher average wind velocity (see Fig. 2.3), and hence probably also from the cooling effect of foliage transpiration (Wieser 2002).

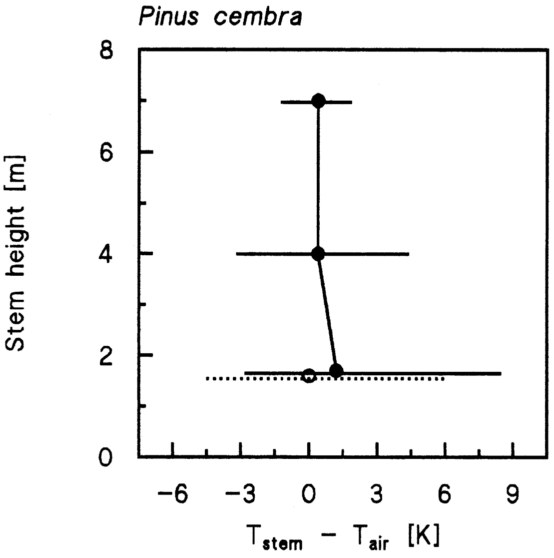

Fig. 2.6. Annual mean temperature difference between stem and air temperature at the south (closed symbols) and the north side (open symbol) of a *Pinus cembra* tree in relation to stem height. The horizontal bars indicate the range of daily maximum overheating and daily maximum undercooling within an entire year. Measurements were made at Mt. Patscherkofel (Klimahaus), Austria, 1950 m a.s.l. (After Wieser 2002.)

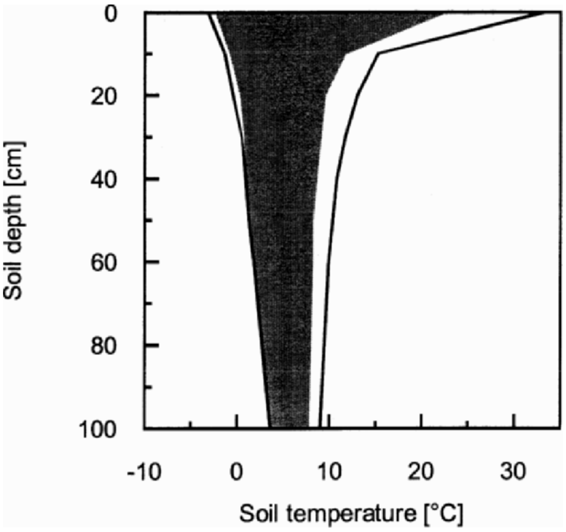

Fig. 2.7. Seasonal amplitude of maximum and minimum soil temperatures under a closed *Pinus cembra* forest (black area) and in a nearby clearing with low stature vegetation (white area). Measurements were made at Obergurgl, Austria, 1920 m a.s.l. (Modified after Aulitzky 1961b.)

Beside canopy temperatures, soil temperature is of equal importance for the altitudinal position of the treeline (Körner and Paulsen 2004). Compared to air temperature, however, soil temperature data within the timberline ecotone are often hardly comparable because soil temperature is influenced by many factors, among then soil texture, bulk density, soil moisture, heat conductivity, exposure to wind and radiation, and the type of vegetation cover to name the probably most important ones (Neuwinger 1980; Häsler et al. 1999; Holtmeier 2003; cf. also Fig. 2.2).

Soil temperature generally decreases rapidly with increasing soil depth. For example, maximum root zone temperature under a closed canopy at treeline in the central Austrian Alps in Obergurgl, Ötztal at 1920 m above sea level decreased from 22.5 °C at 1 cm soil depth to 11.7 °C at 10 cm soil depth, and was only 7.7 °C at 100 cm soil depth (Fig. 2.7).

Under a snow cover soil temperature generally does not drop far below zero. Thus, the annual temperature amplitude under the canopy of this subalpine forest is close to 25 K at 10 cm and is reduced to less than 9 K at 100 cm soil depth (Aulitzky 1961b; Fig. 2.7). Data recently collected from 12 treeline sites in the eastern and western European Alps indicate that soil temperature at 10 cm soil depth under tree canopies varies between close to +15 °C during the summer and -5.0 °C during the winter, and the growing season mean is 7.0 ± 0.4 °C (Körner and Paulsen 2004).

Soil temperatures under canopies of adult trees covering the ground and hence creating a "*forest microclimate*", generally do not differ significantly with respect to slope exposure and the variability in the growing season mean between north and south exposed slopes is commonly less than 0.5 K (Körner and Paulsen 2004). These findings are in line with Innerebner (1933) who documented the same for air temperature 2 m above ground on north and south slopes in the central Alps. Slope contrasts however, come into play in seedling and low stature vegetation cover. Differences in mean growing season topsoil temperature between south and north facing slopes can be up to 2.5 K as shown for an afforestation at Stillberg, Switzerland at 2185 m above sea level (Häsler et al. 1999), and may even be up to 4.4 K in low stature vegetation as shown for the timberline ecotone within the central Austrian Alps by Kronfuss (1972).

Since closed tree canopies prevent soil heat flux and radiative warming their root zone is significantly colder than the ground under adjacent low stature vegetation. For example, at the upper timberline in Obergurgl, Ötztal (Austria) at 2050 m above sea level growing season soil temperature in 10 cm depth were nearly 3 K lower under a closed *Pinus cembra* forest as compared to an adjacent clearing with low stature vegetation (Aulituki 1961b; cf. also Fig. 2.7). Similar differences in top soil temperatures between forested and adjacent unforested sites were also observed at the treeline in the Bolivian Andes (Kessler and Hohnwald 1998) and the eastern Cordilliera of Equador (Bendix and Rafiqpoor 2001). Additionally, small scale variations in soil temperature under low stature vegetation within the timberline ecotone in a certain geographical region can be up to 8 K due to differences in microtopography, wind, vegetation cover, and soil type (Neuwinger 1980; see also Fig. 2.3).

Figure 2.7 also shows that at snow covered sites the low heat conductivity of the snow inhibits the penetration of sub-freezing temperatures into the soil. Furthermore, early snowfall before the soil is frozen results in unfrozen soils throughout the winter (Aulitzky 1961b; Havranek and Tranquillini 1995; Wieser 2004). By contrast, if the snow cover is missing or thin, soil water may freeze to a depth of 1 m and soil frost may last for nearly 5 months as was observed at the upper timberline in the Austrian (Aulitzky 1961b) and in the Swiss Alps (Turner et al. 1975; Turner and Blaser 1977; Schönenberger and Frey 1988).

Taken together, given their life form, trees at timberline are well coupled to the atmosphere and thus experience lower tissue temperatures than adjacent low stature vegetation. As a consequence, their apical meristems do not profit from radiative warming. In addition, a tree's canopy prevents heat flux to their rooting zone and hence soil temperatures are also lower as compared to *krummholz*-mats and other low stature vegetation. Thus, temperature is suggested to be the key factor in determining the transition from forests to alpine shrub and grassland and determining the upper limit of tree life.

References

Aulitzky H (1961a) Über die Windverhältnisse einer zentralalpinen Hangstation in der subalpinen Stufe. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 209-230

Aulitzky H (1961b) Die Bodentemperaturverhältnisse in der Kampfzone oberhalb der Waldgrenze und im subalpinen Zirben-Lärchenwald. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 153-208

Aulitzky H (1963) Grundlagen und Anwendung des vorläufigen Wind-Schnee-Ökogramms. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 60: 765-834

Aulitzky H (1984) The microclimatic conditions in a subalpine forest as basis for the management. Geo Journal 8: 277-281

Baig MN, Tranquillini W (1980) The effects of wind and temperature on cuticular transpiration of *Picea abies* and *Pinus cembra* and their significance in desiccation damage at the alpine treeline. Oecologia 47: 252-256

Barry RG (1979) High altitude climates. In: Webber PJ (ed) High altitude geoecology. Westview Press, Boulder, pp 55-74

Barry RG (1992) Mountain weather and climate. Methunen, London

Barry RG, Van Wie CC (1974) Topo- and microclimatology in alpine areas. In: Ives JD, Barry RG (eds) Arctic and alpine environments. Metuhen, pp 73-83

Baumgartner A (1980) Mountain climates from a perspective of forest growth. In: Benecke U, Davis MR (eds) Mountain environments and subalpine forest growth. Proceedings IUFRO Workshop November 1979 Christchurch, New Zealand. New Zealand Forest Service, Wellington, Technical Paper No. 70, pp 27-39

Bendix J, Rafiqpoor MD (2001) Studies on the thermal conditions of soils at the upper tree line in the Páramo of Papallacata (Eastern Cordillera of Equador). Erdkunde 55: 257-276

Beniston M (1997) Variations of snow depth and duration in the Swiss Alps over the last 50 years: links to changes in large-scale climate forcing. Climatic Change 34: 281-300

Brockmann-Jerosch H (1919) Baumgrenze und Klimacharakter. Pflanzengeographische Kommission der Schweizerischen Naturforschenden Gesellschaft. Beiträge zur Landesaufnahme 6. Rascher und Cie, Zürich

Caldwell MM (1970) The wind regime at the surface of the vegetation layer above timberline in the Central Alps. Centralblatt für das Gesamte Forstwesen 87: 65-74

Dirmhirn I (1964) Das Strahlungsfeld im Lebensraum. Akademische Verlagsgesellschaft, Frankfurt

Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. Verlag Eugen Ulmer, Stuttgart

Fliri F (1975) Das Klima der Alpen im Raume von Tirol. Monographien zur Landeskunde Tirols I. Universitätsverlag Wagner, Innsbruck, München

Fliri F (1992) Der Schnee in Nord- und Osttirol 1985-1991. Universitätsverlag Wagner, Innsbruck

Franz H (1979) Ökologie der Hochgebirge. Ulmer, Stuttgart

Frei Ch, Schär Ch (1998) A precipitation climatology of the Alps from high-resolution rain-gauge observations. International Journal of Climatology 18: 873-900

Friedel H (1961) Schneedeckendauer und Vegetationsverteilung im Gelände. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 317-369

Friedel H (1967) Verlauf der alpinen Waldgrenze im Rahmen anliegender Gebirgsränder. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 75: 81-172

Friedland AJ, Boyce RL, Webb ET (1992) Winter and early spring microclimate of a subalpine spruce-fir forest canopy in central New Hampshire. Atmospheric Environment 26A: 1361-1369

Geiger R (1961) Das Klima der bodennahen Luftschichten. Viehweg, Braunschweig

Grabherr G (1997) The high mountain ecosystems of the Alps. In: Wiegloaski FE (ed) Polar and alpine tundra ecosystems of the world. Elsevier, Amsterdam, pp 97-121

Grace J, Allen SJ, Wilson C (1989) Climate and the meristem temperatures of plant communities near the tree-line. Oecologia 79: 198-204

Gross M (1989) Untersuchungen an Fichten der alpinen Waldgrenze. Dissertationes Botanicae 139. Cramer, Berlin, Stuttgart

Gunsch J (1972) Vergleichende ökologische Untersuchungen von Kleinstandorten im Bereich der subalpinen Zirben-Waldgrenze. Ph.D. thesis, Innsbruck University

Hadley JL, Smith WK (1987) Influence of krummholz mat microclimate on needle physiology and survival. Oecologia 73: 82-90

Häsler R, Streule A, Turner H (1999) Shoot and root growth of young *Larix decidua* in contrasting microenvironments near treeline. Phyton 39: 47-52

Havranek WM, Tranquillini W (1995) Physiological processes during winter dormancy and their ecological significance. In: Smith WK, Hinckley TM (eds) Ecophysiology of coniferous forests. Academic Press, San Diego, pp 95-124

Holtmeier F-K (2003) Mountain timberlines. Ecology, patchiness, and dynamics. Advances in Global Change Research, vol 14. Kluwer Academic Publishers, Dordrecht, Boston, London

Innerebner F (1933) Über den Einfluß der Exposition auf die Temperaturverhältnisse im Gebirge. Meteorologische Zeitschrift 50: 337-346

Kessler M, Hohnwald S (1998) Soil temperatures inside and outside forested treeless boulder slopes in the Bolivian high Andes. A test of the hypothesis of Walter and Medina 1969. Erdkunde 52: 54-62

Körner Ch (2003) Alpine plant life: functional plant ecology of high mountain ecosystems, 2nd edn. Springer, Berlin

Körner Ch, Paulsen L (2004) A world-wide study of high altitude treeline temperatures. Journal of Biogeography 31: 713-732

Kronfuss H (1967) Schneelage und Ausaperung an der Waldgrenze. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 75: 207-241

Kronfuss H (1970) Räumliche Korrelation zwischen der Windstärke in Bodennähe und der Schneedeckenandauer. Centralblatt für das Gesamte Forstwesen 87: 99-116

Kronfuss H (1972) Kleinklimatische Vergleichsmessungen an zwei subalpinen Standorten. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 96: 159-176

Kronfuss H (1997) Das Klima einer Hochlagenaufforstung in der subapinen Höhenstufe - Haggen im Sellraintal bei St. Siegmund, Tirol (Periode 1975-1994). Schriftenreihe der Forstlichen Bundesversuchsanstalt Wien, FBVA Bericht 100

Kronfuss H, Stern R (1978) Strahlung und Vegetation. Angewandte Pflanzensoziologie 24. Forstlichen Bundesversuchsanstalt Wien

Kronfuss H, Havranek WM (1999) Effects of elevation and wind on the growth of *Pinus cembra* L. in a subalpine afforestation. Phyton 39: 99-106

Kuhn H (1997) Meteorologische und klimatologische Bedingungen für die Flora und Fauna von Nordtirol, Osttirol und Vorarlberg, In: Polatschek A (ed) Flora von Nordtirol, Osttirol und Vorarlberg, Band 1. Tiroler Landesmuseum Ferdinandeum, pp 26-42

Larcher W (1985) Winter stress in high montains. In: Turner H, Tranquillini W (eds) Establishment and tending of subalpine forest: research and management. Berichte Eidgenössische Anstalt für das forstliche Versuchswesen Birmensdorf 270, pp 11-19.

Larcher W (2001) Ökophysiologie der Pflanzen: Leben, Leistung und Stressbewältigung der Pflanzen in ihrer Umwelt. Ulmer, Stuttgart

Larcher W, Wagner J (2004) Lebensweise der Alpenrose in ihrer Umwelt: 70 Jahre ökophysiologische Forschung in Innsbruck. Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck 91: 251-291.

Lauscher F (1976) Weltweite Typen der Höhenabhängigkeit des Niederschlags. Wetter und Leben18: 80-90

Loris K (1981) Dickenwachstum von Zirbe, Fichte und Lärche an der alpinen Waldgrenze/Patscherkofel. Ergebnisse der Dendrometermessungen 1976/79. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 142: 417-441

Loris K, Havranek WM, Wieser G (1999) The ecological significance of thickness changes in stem, branches, and twigs of *Pinus cembra* L. during winter. Phyton 39: 117-122

Markart G (2000) Der Wasserhaushalt von Hochlagenaufforstungen. Schriftenreihe der Forstlichen Bundesversuchsanstalt Wien, FBVA Bericht 117

Nägeli W (1971) Der Wind als Standortfaktor bei Aufforstungen in der subalpinen Stufe. Schweizerische Anstalt für das forstliche Versuchswesen 47: 33-147.

Neuwinger I (1970) Böden der subalpinen und alpinen Stufe in den Tiroler Alpen. Mitteilungen der Ostalpin-Dinarischen Gesellschaft für Vegetationskunde 11: 135-150

Neuwinger I (1980) Erwärmung, Wasserrückhalt und Erosionsbereitschaft subalpiner Böden. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 139: 113-144

Neuwinger-Raschendorfer I (1961) Bodenfeuchtemessungen. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 257-264

Pruzer E (1965) Beiträge zur subalpinen Waldforschung. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 66

Sauberer F, Dirmhirn I (1958) Das Strahlungsklima. In: Steinhauser F, Eckel O, Lauscher F (eds) Klimatographie von Österreich. Springer, Wien, pp 13-102

Schmidli J, Schmutz, Ch, Frei Ch, Wanner H, Schär Ch (2002) Mesoscale precipitation variability in the region of the European Alps during the 20th century. International Journal of Climatology 22: 1049-1074

Schönenberger W, Frey W (1988) Untersuchungen zur Ökologie und Technik der Hochlagenaufforstung. Forschungsergebnisse aus dem Lawinenanrissgebiet Stillberg. Schweizerische Zeitschrift für Forstwesen 139: 735-820

Schröter C (1926) Das Pflanzenleben der Alpen. Eine Schilderung der Hochgebirgsflora. Verlag Albert Raustein, Zürich

Steinhauser F, Eckel O, Lauscher F (1960) Klimatographie von Österreich. Springer, Wien, pp 137-380

Svoboda J (1977) Ecology and primary production of raised beech communities, Truelove Lowland In: Bliss LC (ed) Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. University of Alberta Press, Edmonton, pp 185-216

Tranquillini W (1964) Photosynthesis and dry matter production of tress at high altitudes. In: Zimmermann MH (ed) The formation of wood in forest trees. Academic Press, New York, pp 505-518

Tranquillini W (1979) Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. Ecological Studies, vol 31. Springer Berlin, Heidelberg, New York

Tranquillini W, Turner H (1961) Untersuchungen über die Pflanzentemperaturen in der subalpinen Stufe mit besonderer Berücksichtigung der Nadeltemperaturen der Zirbe. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 127-151

Turner H (1958a) Maximaltemperaturen oberflächennaher Bodenschichten an der subalpinen Waldgrenze. Wetter und Leben 10: 1-12

Turner H (1958b) Über das Licht- und Strahlungsklima einer Hochlage der Ötztaler Alpen bei Obergurgl und seine Auswirkung auf das Mikroklima und auf die Vegetation. Archiv für Meteorologie, Geophysik und Bioklimatologie 8B: 273-325

Turner H (1961) Die Niederschlags- und Schneeverhältnisse. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 265-315

Turner H (1970) Grundzüge der Hochgebirgsklimatologie. In: Ladurner J, Purtscheller F, Reisigl H, Tratz E (eds) Die Welt der Alpen. Pinguin Verlag, Innsbruck, pp 170-182

Turner H (1993) Alpine microclimates: typology and examples. In: Anfodillo T, Urbinati C (eds) Ecologia delle foreste di alti quota. Corso di cultura in ecologia 30. University Padua, pp 27-34

Turner H, Blaser P (1977) Mikroklima, Boden und Pflanzen an der oberen Waldgrenze. Eidgenössische Anstalt für das Forstliche Versuchswesen 61: 757-765

Turner H, Rochat P, Streule A (1975) Thermische Charakteristik von Hochlagenstandorten im Bereich der oberen Waldgrenze (Stillberg, Dischmatal bei Davos). Mitteilungen der Eidgenössischen Anstalt für das Forstlichen Versuchswesen Birmensdorf 51: 95-119

Veit H (2002) Die Alpen – Geoökologie und Landschaftsentwicklung. Ulmer, Stuttgart

Wieser G (1997) Carbon dioxide gas exchange of cembran pine (*Pinus cembra*) at the alpine timberline during winter. Tree Physiology 17: 473-477

Wieser G (2002) The role of sapwood temperature variations within *Pinus cembra* on calculated stem respiration: implications for upscaling and predicted global warming. Phyton 42: 1-11

Wieser G (2004) Seasonal variation of soil respiration in a *Pinus cembra* stand in the Central Austrian Alps. Tree Physiology 24: 475-480

Wieser G, Bahn M (2004) Seasonal and spatial variation of woody tissue respiration in a *Pinus cembra* tree at the alpine timberline in the central Austrian Alps. Trees 18: 576-580

Wieser G, Gigele T, Pausch H (2005) The carbon budget of an adult *Pinus cembra* tree at the alpine timberline in the Central Austrian Alps. European Journal of Forest Research 124: 1-8

3 Soils - Heterogeneous at a Microscale

Dieter Stöhr

Abteilung Forstorganisation, Amt der Tiroler Landesregierung, Innsbruck

3.1 Introduction

Soil properties are influenced by climate, vegetation, fauna, relief, geological substrate, and time (Jenny 1941). Most of theses soil-forming parameters vary according to the altitudinal change of climatic conditions. In contrast to lowland soils, the influence of micro-topography gains importance at timberline: Soil moisture and temperature, vegetation, even physical soil properties such as grain size, water potential or bulk density are influenced by the relief, forming a complex pattern of soil types and humus forms, which seem to be a characteristic feature for soils at timberlines (Holtmeier 2003).

An irregularly shaped snow-pack plays a key role regarding this small scale variability of soils, influencing precipitation, leaching of plant nutrients, soil temperature, soil moisture, and erosion processes.

Vegetation varies from closed forests to tree islands, dwarf shrub, turf, and bog communities. C/N-ratios of biomass is closely related to these plant communities and varies from 45 - 50 in dwarf shrubs to 25 in grass species (Hiller 2001). As a result of small scale variation of ecological parameters, decomposition rates of soil organic matter varies on a microscale, altering humus forms from mull to mor within a meter (Neuwinger 1965; Bednorz 2000). These changes are not restricted to the humus layer, but have an effect on mineral soil pedogenesis. On siliceous parent material a whole series from lithic leptosols, dystric cambisols to haplic podzols can be observed frequently at the same site (Neuwinger 1965).

A feature, common to most high mountain areas is that they lost any old soil cover during the latest glacial advances. Only some areas in the very

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eastern parts of the Alps were not covered with glaciers during the Würm-period of the Pleistocene (Van Husen 1987). So, most of the soils at timberline are relatively young.

Due to differences in these ecological parameters it is obvious, that a wide range of soil types and humus forms is present in the timberline ecotone within small areas.

3.2 Specific pedogenetic factors at the timberline

3.2.1 Parent material

Due to the geological heterogeneity of the European Alps, a large diversity of parent materials is the basis for pedogenesis in the timberline ecotone. The Eastern Alps consist of a central mass of crystalline and schistose rocks flanked on each side by a zone of Mesozoic beds consisting largely of limestone with minor shares of sandstones and marls.

Glaciations has altered the original rock structure and shape of the landscape, leaving glacial deposits as soil parent material in many places.

Wind lain silt from young moraines without vegetation cover, may have contributed to the silt and clay fraction of timberline soils especially on leeward, wind sheltered microsites.

Retzer (1974) summarizes the soil parent material of alpine areas as “medium to coarse textured, relatively thin, heterogeneous and only weakly weathered”. Parent material for soil development is also subjected to considerable local movement by frost action, free fall, slope creep and water movement.

3.2.2 Precipitation

Precipitation in mountains generally increases with altitude. Annual precipitation at timberline in the European Alps ranges from 800 to 2600 mm year^{-1} (Turner 1961) at a mesoscale, with highest values in the northern and southern rim and low levels in the rain shadowed inner Alps. While the microscale distribution of precipitation is rather uniform in the area of closed subalpine forests, the variation multiplies in the timberline ecotone where tree islands, ridges and small valleys influence the wind field.

Snowpack

30 – 50 % of annual precipitation at timberline is snow (Turner 1961). Topography strongly influences the pattern of winter snow deposition, as well as the exposure to wind and sun. So landform features such as depressions, hillsides and mountains or trees, rising over the snow surface are crucial for snow distribution. Snow accumulates in the lee of certain landform features and persists much longer than on wind swept ridges (Fig. 3.1).

The accumulation and persistence of snow in patches seems to be characteristic for the alpine timberline. These topographically induced snowmelt gradients are highly consistent and predictable throughout the years (Stanton et al. 1994).

This heterogeneous snow cover influences vegetation communities, humus forms and soil types, following the isolines of snowmelt (Aulitzky 1963a; Bowmann 1992; Körner 1999). The influence of snow on vegetation has been well studied and Helm (1982) divided it into four factors:

- Insulation of vegetation
- Shortened growing season
- Source of melt-water
- Soil movement

Further effects are the mechanical effects of snow accumulation on steep slopes and the elution of ions from the snow-pack.

Snow height may vary at the beginning of the ablation period from zero to more than 200 cm within meters (Turner 1961; Hiemstra et al. 2002), which means differences in soil moisture for most of the growing season.

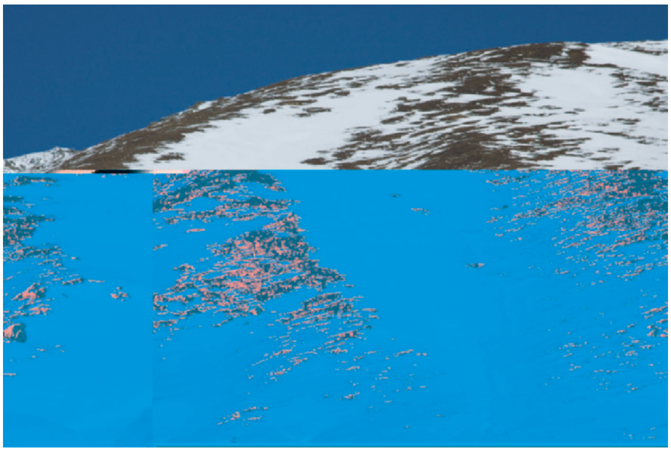

Fig. 3.1. Snow distribution at a timberline site near Haggen, Tyrol (E: 11°05.135', N: 47°12.690').

Additionally, sites with snow accumulation in winter tend to have lower moisture loss by dry winds during the growing season (Neuwinger-Raschendorfer 1963). Over the long term, consistent differences in snowmelt can have important consequences for soil development. Soil nitrogen and phosphorus content tends to decrease in late-melting sites (Stanton et al. 1994). Enhanced leaching of bases and changed decomposition rates are some other possible effects on soil formation.

Deposition of air pollutants

Timberline sites are often described as "background sites", indicating that the influence of atmospheric pollutants is rather low, because timberline sites are often far away from emission sources and nitrogen in wet deposition decreases in general with altitude. The annual input of total nitrogen ranges from 5 to 40 kg N ha^{-1} a^{-1} at lower altitudes and decreases towards the treeline to 5 to 20 kg N ha^{-1} a^{-1}. At timberline dry and occult deposition gains importance and may add more than 20 % to total nitrogen input (Smidt 1996; Herman et. al. 2004).

Considering repeating patterns of snowdrift in the same location year after year, this nitrogen input by meltwater from the snow-pack might influence nitrogen cycling and export in timberline soils. Nitrogen leached from the snow-pack may attribute 15 to 100 % of the potential total atmospheric inputs of N compared to estimations of bulk deposition, depending on snow depth and duration (Bowmann 1992). Brooks et al. (1999) showed that nitrogen is leached from soils with a very short duration of snow cover, due to low heterotrophic activity in these soils, being frozen most of the year. Whereas soils, which are well covered with a snow-pack for months act as nitrogen sinks due to microbial activity in the thawed soils under the snow-pack. Sites characterized by a very long lasting snow pack, release most of the NO_3^-, stored in the snow-pack, to streamflow, due to limited microbial activity in these water saturated soils (Brooks et al. 1999).

3.2.3 Soil moisture

Due to high precipitation and low evapotranspiration, soil moisture is a growth limiting factor for timberline trees only in special cases during summer (Tranquillini 1979). Net photosynthesis starts to decline when soil moisture is below 30 % volume and water potential is below -0.05 MPa (Havranek and Beneke 1978). Neuwinger-Raschendorfer (1963) measured soil water content in the Inner Ötztal in Tyrol, one of the driest Inner Al pine regions and found water contents seldom below 20 % volume, soil water potential was always > -0.1 MPa. Neuwinger-Raschendorfer (1963) showed, that not only soil properties and precipitation, but also the exposure against wind influences soil moisture content on a small scale, making north faced, wind exposed slopes even drier than south facing ones. With the exception of snow bed communities, where stagnant water in the topsoil is present during most of the growing season, decomposition rates are not reduced due to excess soil moisture in timberline soils and are not substantial for site development (Bednorz 2000; Rehder 1970). On sites with very high soil moisture content throughout the season the increasing respiration with higher soil temperatures is restricted (Stottlemyer et al. 2001).

Soil moisture content also influences pedogenesis. Fitze (1980) showed at moraine soils of the Steingletscher in Switzerland, that dystric cambisols have developed at sites with a shorter snow cover, whereas sites with long lasting snow-packs show clear podzolization.

3.2.4 Soil temperature

Soil temperatures are influenced by factors such as slope aspect and inclination, soil moisture, plant cover, duration of winter snow-pack, humus content, soil texture, porosity, and bulk density.

Soil temperatures below 7 °C reduce net photosynthesis and root growth (Havranek 1972). Temperatures below this limit are frequent at timberlines even during summer especially at wind swept ridges with low vegetation cover, north facing slopes, and snow bed soils. Aulitzky (1963a) showed that soils under closed forests are significantly colder during the growing season than soils in clearings at the same site.

Bednorz (2000) found, that different decomposition rates can be attributed to differences in soil temperature for sites with mor as dominating humus form, whereas on sites in gullies with much higher decomposition rates the quality of organic matter (C/N ratio) is more important than differences in soil temperature. Microsites at the timberline show a characteristic soil temperature regime, which modifies the decomposition rate of organic matter (Hiller 2001). Sjögersten (2003) found positive correlations between soil temperature and respiration in tundra and forest soils in Norway.

Soil temperatures during wintertime are controlled by snow distribution. Sites well covered with snow for the whole winter show temperatures near 0 °C, whereas windswept sites with poor or no snow cover show minimum temperatures near –20 °C in the top soil and freeze to more than 1 m depth. Even in summer these wind swept sites show significantly lower temperatures due to the presence of cooling winds (Aulitzky 1963b). Small areas on south facing slopes with little advection are characterized by thermal heating during clear days in summer. Maximum temperatures in the topsoil can reach more than 60 °C, which may be lethal for plants, leaving small patches without vegetation.

3.2.5 Erosion processes and soil age

In the European Alps erosion processes structure the slopes, forming a complex terrain. Especially on steep slopes, erosion processes play a key role in pedogenesis (Gracanin 1972). Buried or truncated soil profiles, indicating erosion processes, can be found in many sites, so different stages of soil development appear in complex patterns at a microscale.

Therefore many soils can only reach initial stages of soil development and are rather young. Investigations from moraine soils in Switzerland indicate that podzolisation with infiltration of organic substances takes 1000 to 3000 years on siliceous parent material (Fitze 1980; Heikinnen 1980).

Other frequent reasons for small scale variations in soil properties are the redistribution of organic matter and soils by avalanches on steep slopes (Gracanin 1972). In the steep terrain of the alpine timberline snow gliding and glide-avalanches are a frequent phenomenon. Under certain circumstances these snow movements induce soil erosion when grasses, shrubs or young trees are torn away with the gliding snow (Fig. 3.2). These injuries of the plant cover may be starting points for further erosion processes (Newesely et al. 2000) and thus may also change site characteristics and may degrade soils especially in the starting zone of avalanches.

Fig. 3.2. Soil erosion by an avalanche.

Whenever bare soil is present, great quantities of fine earth material can be easily eroded, especially during spring snowmelt and summertime storms. Dust erosion was an important process, when today's timberline was part of the glacier foreland but lost influence with the establishment of a more or less closed vegetation cover.

Erosion processes in the timberline ecotone of the European Alps were often linked with periods of massive deforestation by fire, clearance, and browsing as Neuwinger-Raschendorfer (1963) showed for the timberline ecotone in the Tyrolean Ötztal. Tasser et al. (2003) showed enhanced landslide activity due to land use changes in subalpine study sites in Northern and Southern Tyrol.

3.2.6 Permafrost

Solifluction and cryoturbation processes had a strong influence on pedogenesis at the timberline. Periglacial cover-beds in the alpine zone can be attributed to different periods during the Holocene, whereas periglacial beds in the subalpine zone developed in the earlier periods of the Pleistocene (Veit et al. 2002).

Under certain circumstances even today, soils influenced by permafrost may be found on north facing slopes below the timberline (Kneisel et al. 2000), impeding tree growth on sites with perennial frozen soils (Fig. 3.3).

Fig. 3.3. Soil formed by solifluction, with frozen soil 60 cm below surface, Radstätter Tauern, 1800 m above sea-level, Coordinates (WGS 84): N: 47°^8,894’, E: 13°22,701’. (Photo: K. Katzensteiner, University of Natural Resources and Applied Life Sciences, Vienna.)

3.2.7 Vegetation and soil

In the complex alpine terrain it is hard to decide to what extent vegetation is a consequence of soil properties or to what extent vegetation influences soil properties. There are some indications from tundra ecosystems with a more homogenous morphology, which indicate, that the presence of trees may influence soil properties. Soils under tree islands show significantly lower bulk densities but higher carbon concentrations, the total carbon amounts in the topsoil may be 20 % lower under tree islands than in the neighbouring tundra (Pauker, 1996).

Vegetation communities influence pedogenesis by a number of processes. Trees rising above the winter snow pack influence the wind field resulting in downwind snowdrifts, changing soil temperatures and soil moisture throughout the year (see Chap. 2). In loose forest stands with low canopy cover, snow accumulates compared to terrain without trees. Dense tree islands act differently, relatively little snow is trapped inside the tree groups, whereas big snowdrifts accumulate downwind (snow fence effect). Theses compact snow drifts often persist until summer. High soil moisture contents and long lasting low soil temperatures strongly influence these soils (Holtmeier 2003).

C/N ratio of litter strongly influences decomposition of organic matter resulting in humus forms and soil types being in close relation to the vegetation community (Neuwinger-Raschendorfer 1963; Hiller 2001; Bednorz 2000).

A number of studies across the European Alps found a sharp decrease of soil charcoal mass, correlated with the upper altitudinal limit of podzols indicating the position of the uppermost tree limit during the Holocene (Carnelli et al. 2004; Neuwinger-Raschendorfer 1963). These former forest soils still show specific features such as a distinct podzolisation which could only develop under a forest cover, limiting decomposition of organic matter.

3.2.8 Timberline fluctuations

Radiocarbon dating of soil charcoal fragments indicates that the timberline ecotone has changed its position during the Holocene for several times due to climatic changes and man made slash-and-burn and pastoral practices. The tree-line reached its maximum elevation in the Swiss Northern Alps (about 2250 m a.s.l.) between ca. 6000 and 3500 years before present (BP) (Wick et al. 2003) considerably later than in the Central and Southern

Alps, where the maximum elevation of 2700 m was reached between 8000 and 5000 years BP (Carcaillet 2000).

At present, treeline is 200-300 meters beyond the maximum limit reached in mid-late Holocene (Carcaillet 2000; Wick et al 2003). On siliceous parent material the presence of Podzols under dwarf shrub communities is often interpreted as indicators for the presence of a forest canopy in the past (Neuwinger-Raschendorfer 1963).

Holtmeier (2003) gives on overview of the amount of man made deforestation in the timberline ecotone of the European Alps. Local climate and topography have controlled human influence, in particular slopes with southern exposure became completely deforested.

3.2.9 Grazing

Human influence on the timberline ecotone of the European Alps starts 7000 years BP in the Southern Alps (Bätzing 2003). With increasing importance of life stock farming during the Subboreal (5000 - 2500 years BP), human influence on timberline ecosystems gained importance (Bortenschlager 1984; Stumböck 1999). In many regions present timberline is far below the potential timberline due to high grazing pressure. Grazing by domestic animals such as cattle, sheep, and goats prevents natural regeneration and influences soil properties. Main effects of grazing on soil properties are: soil compaction and high surface run off (Markart et. al. 2004), increased decomposition rates, improved plant availability of nutrients, reduced amounts of nutrients stored in the soil, as long as soils are not fertilized, changed spatial distribution of nutrients, and reduced soil pH-values by net export of base cations.

Excessive grazing may also cause growing percentage of bare soils and increased soil erosion.

3.3 Soil types and humus forms

Soil formation at timberline is usually slow and lasted for only 12000 years or less. Steep slopes are shaped by erosion, especially if stabilising vegetation is absent. So, many soils are in a constant process of rejuvenation. As a result, poorly developed soils are omnipresent in high mountain areas.

Although soil forming processes depend at least partially on the altitudinal change of climatic conditions, no single soil type can be considered typical for the timberline ecotone. On a microscale, effects of microtopography, microclimate, soil age, and plant cover strongly modify pedogenesis.

Figure 3.4 shows a soil map from a timberline site on siliceous parent material near Obergurgl, Ötztal, 2040 – 2240 m a.s.l.

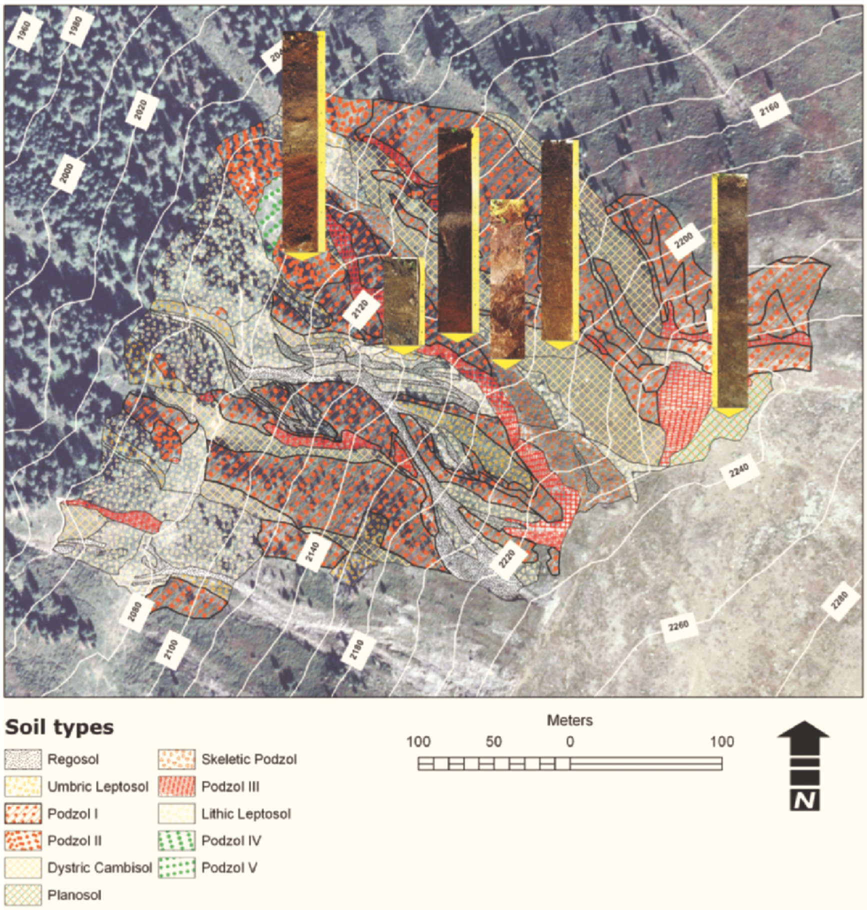

Fig. 3.4. Soil map at a timberline site near Obergurgl, Ötztal 2040 – 2240 m a.s.l. Podzols were subclassified in this survey into 5 different subtypes: Podzol I: Podzol with a Bh horizon, humus type: mor humus; Podzol II: Podzol without Bh-Horizon, humus type: mor humus; Podzol III: Podzol with partially wind eroded humus layer and A-horizon; Podzol IV: Podzol under grassland, with a Bh-horizon, humus type: moder; and Podzol V: Podzol under grassland, without a Bh-horizon, humus type: moder. (Redrawn after Neuwinger-Raschendorfer 1963; ortophoto: Land Tirol 2003.)

A process characteristic for cold and moist environments is the accumulation of a humus layer. Decomposition of organic material is delayed and at least the top soil tends to be acidified because the recycling of plant products is delayed. Most soils in the timberline ecotone are shallow and rich in skeletal material and humus. Due to low activity of soil fauna, bioturbation seems to be less important than in the area of closed forests (Carcaillet 2000). Soils were named according to the World Reference Base for Soil Ressources 1998 (Bailly et al. 2001; Nestroy 2002). Humus classification was done according to the "New European humus classification system" presented by Jabiol et al. (2004).

3.3.1 Soils on siliceous parent material

Leptosols

Unstable rocky slopes and outcrops of bedrock are common features in mountainous and formerly glaciated regions, so Leptosols are particularly common at timberline. Very shallow soils over hard rock and soils that are extremely stony can be described as Leptosols. Leptosols are azonal soils with an incomplete solum and without clearly expressed morphological features. Leptosols are free draining soils, their water holding capacity is limited. The parent material and the climate influence strongly the physical, chemical, and biological properties of Leptosols. The excessive internal drainage of many Leptosols can cause drought even in a humid environment. In many systems Leptosols on acid rock are also called `Rankers'.

- Soil profile: A(B)C

Lithic Leptosols are present in the timberline ecotone where solid, slowly weathering rock, or slope erosion inhibit the development of a B-horizon.

- Humus: The accumulation of organic matter is limited due to limited time for pedogenesis and the low productivity of dwarf shrubs. Therefore only initial humus horizons have developed.
- Soil Profile: OL-OF-(OHz)-Ajz-C
- The vegetation on these poor soils consists mainly of open communities of dwarf shrubs such as *Vaccinium vitis-idaea*, *Calluna vulgaris*, *Juniperus nana*, and *Rhododendron ferrugineum* (Neuwinger 1965). Nutrient pools and availability are very low.

Lithic Leptosols may appear also at microsites affected by wind erosion: Under theses conditions, the topsoil is typically poor in humus due to litter erosion by strong winds and low productivity of vegetation communities.

Low soil moisture contents throughout the year and low soil temperatures restrict decomposition of organic matter due to the limited water storage capacity and the absence of a snow-pack for most of the winter (Turner 1961). The absence of sheltering snow-pack in winter, low soil temperatures, and soil moisture inhibit tree growth on these soils.

- Vegetation communities: Loiseleurio-Vaccinion, Loiseleurio-Cetrarietum, Gymnomitrio-concinnati-Loiseleurietum procumbentis (Grabherr et al. 1993).

Umbric Leptosols With ongoing accumulation of organic matter, Umbric Leptosols develop. Water capacity of theses soils is still rather low, which may be compensated by high precipitation rates, unless snow erosion limits winter precipitation. Low amounts of fine material, early stages of soil weathering and minor amounts of Ca, K, and Mg in the parent material mean restricted amounts of theses elements for plant nutrition (Rehfuess 1990)

- Moder to mor humus are the prevalent humustypes.
- Soil Profile: OL-OF-OHm-Ajz/Aze-(B)C
- Vegetation communities: Empetro-Vaccinietum gaultherioidis, Juniperion nanae, Rhododendro ferruginei-Pinetum prostratae). On sites with well developed mor humus, open stands of *Pinus cembra*, *Picea abies* and *Larix decidua*, may establish. Closed stands of *Pinus mugo* can be observed and are sometimes interpreted as a consequence of medieval slash-burns in closed cembran forests (Grabherr et al. 1993).

Regosols

Poorly developed soils on unconsolidated, finely grained material with an ochric surface horizon can be described as Regosols. Glacial deposits, rich in fine material often form the parent material. Their surface horizon contains poorly decomposed organic matter. Low coherence of the mineral soil makes most Regosols in sloping areas prone to erosion. Low water holding capacity and high permeability to water make these Regosols also sensitive to drought. Regosols recently formed by slope erosion are poor in humus but usually show slightly higher soil moisture content than Leptosols due to their position in concave terrain with additional wintertime precipitation by snow accumulation. These soils are often covered with open dwarf shrubs (*Juniperus communis*, *Calluna vulgaris*, *Vaccinium vitis-idaea*).

- Soil profile: OL-OF-(OH)-Ajz/Aze-(B)C

On sites with high moisture content throughout the growing season due to excessive wintertime snow drifts and near small river beds Regosols are easily eroded. These sites are often covered by communities with *Alnus viridis* (Grabherr et al. 1993), showing a slightly higher nitrogen content in the top soil and higher decomposition rates.

- Soil profile: OL-OF-Ajz-(B)C

Cambisols

Soils with beginning horizon differentiation, which can be identified from changes in colour, structure or carbonate content, can be described as Cambisols. These soils are characterized by slight or moderate weathering of parent material. Notable quantities of illuviated clay, organic matter, aluminium, and/or iron compounds are missing, which means that Cambisols are still in an early stage of soil formation. Cambisols are medium-textured and have a good structural stability, a high porosity, medium water holding capacity, and good internal drainage. Cambisols have a neutral to weakly acidic soil reaction, a satisfactory chemical fertility and an active soil fauna. Frequent parent materials at the timberline are glacial till and colluvial deposits. Eutric and oligotrophic Cambisols at the timberline are restricted to areas where the forest cover was removed and the sites are/were used as alpine meadows and pastures. As soon as these sites are abandoned, dwarf shrubs invade and replace grassland communities. Within a few decades Dystric Cambisols may develop on these abandoned sites (Tasser et al. 2003).

Dystric Cambisols show some leaching of bases but no clear migration of Fe, Al, organic matter or clay. Moderately acidic Cambisols can be found mostly on sunny slopes under thinly stocked forests with patches of dwarf shrubs (*Juniperus communis*, *Calluna vulgaris*, *Empetrum nigrum*) and bare soil due to solar heating. The transition from the OH-horizon to the underlying Ajz-horizon is gradual. Biogenous intermixing by arthropods dominates over infiltration of humic acids.

These not extremely acidic soils can be found either on sunny slopes, where soil temperatures are higher and the duration of the snowcover is significantly lower than on north facing slopes.

As a consequence of reasonably high microbial activity, moder is the prevalent humus form (Neuwinger-Raschendorfer 1963).

- Soil profile: OL-OF-OH-Ajz(Aze)-B-C

Podzols

Podzols are characterized by an ash-grey horizon bleached by organic acids underneath the humus layer. Complexes of Al, Fe and organic compounds migrate with percolating rainwater from the surface soil to the B-horizon, where the complexes precipitate in an illuvial dark coloured `*spodic*' horizon with brown or black humus and/or reddish iron compounds The overlying soil remains behind as a strongly leached Ae-horizon and a bleached `*albic*' eluvial E-horizon.

Nutrient levels in Podzols are low, because bases are leached from the mineral soil. Plant nutrients are concentrated in the humus layer where they are released by decomposition of organic matter. The humus layer is characterized by acidic pH (1M KCL)-values (2.8 – 3.8) and wide C/N-ratios (35-40). Base saturation and pH-values remain low in the E-horizon and increase slightly in the illuvial Bhs-horizon (Forstliche Bundesversuchsanstalt 1992; Neuwinger-Raschendorfer 1963). Podzols have a sandy texture, with clay contents below 10 % in the E-horizon. Water movement in the soil may be impaired by a dense Bh-horizon. Data from the Austrian Soil Monitoring Programme indicate, that Podzols accumulate more than 50 t C_{org} ha^{-1} in mineral soil and 25 t C_{org} ha^{-1} in the humus layer at an average. The total nitrogen pool for these acidic soils is more than 7000 kg N ha^{-1}, which is not less than in other Austrian forest soil types, but the availability of nitrogen seems to be limited (Forstliche Bundesversuchsanstalt 1992).

The degree of podzolisation depends on:

- slowly weathering parent material,
- high amount of percolating soil water, especially where relief induced accumulation of snowdrifts increases precipitation,
- high soil moisture and low soil temperatures which restricts the decomposition of organic matter,
- wide C/N-ratio of organic litter.

Podzols are typical at timberline on north facing sites with a dense forest cover and on sites with a long lasting snowcover.

- Vegetation communities: Larici-pinetum cembrae, Rhododendretum ferruginei (Grabherr et al. 1993).

Planosols

Soils with bleached, light-coloured, eluvial surface horizons that show signs of periodic water stagnation can be described as Planosols. Their subsoil is slowly permeable and contains more clay than the surface horizon. Planosols are rare on steep slopes and restricted to small flat or concave microsites where additional water and fine material from adjacent slopes influences pedogenesis. The formation of Planosols at timberline is often enhanced by intense cattle grazing (Posch 1980). Easily weathering schists, loamy colluvial and glacial deposits form the parent material.

Stagnic Planosols: Soils with stagnant water occur only in sites with extremely long lasting snow pack and in concave badly drained places, where stagnant water is present during the whole growing season. Trees cannot grow on sites like these due to the duration of the snow cover and very low soil temperatures.

Characteristic plants for snow bed communities, growing in this specific environment are *Salix herbacea*, *Soldanella pulsilla* and *Gnaphalium supinum.*

Other soil types

Histosols may also develop under extremely wet conditions in depressions, where bog communities build up a histic horizon.

3.3.2 Soils on calcareous parent material

Soils on calcareous material develop by physical weathering, solution of carbonates, enrichment of clay minerals and humus accumulation. Carbonate solution accelerates, as the parent material is fragmented by weathering. In some areas the presence of aolean deposits in the topsoil may influence soil development. The accumulation of a thick humus layer depends on three main factors (Bochter 1983):

- parent material: Solid limestone enhances the accumulation of organic material, whereas the presence of a loamy, nutrient rich subsoil within the rooting zone accelerates decomposition rates,
- aspect: on north facing slopes the accumulation of organic matter is far more pronounced than on sunny slopes,
- precipitation: increasing annual precipitation limits decomposition rates.

Lithic Leptosols, Calcaric Regosols

Young soils on steep slopes and on poorly stabilized rock debris under steep mountain walls are abundant in the calcareous Alps. These sites are covered with communities such as Thlaspion rotundifolii, in very initial stages and turf communities such as Firmetum and Seslerio sempervirETUM

(Reisigel et al. 1987). Even early stages of colonization by *Pinus mugo* are possible on these sites, exposed to permanent erosion by rock fall and avalanches.

- Soil profile: OL-OF-OHz-(Az)-C

Rendcic Leptosols, Mollicalcaric Regosols

When the accumulation of organic material continues undisturbedly, a mollic horizon may develop, being 10 to 25 cm thick. This horizon contains or immediately overlies calcaric soil material. This soil type is typical for dense stands of *Pinus mugo* on south facing slopes, single trees of *Picea abies* and *Larix decidua* establish, but are often broken by avalanches, when getting older. The soil profile consists largely of humus, a distinct mineral A horizon is often missing.

Vegetation consists mainly of *Pinus mugo* and dwarf shrubs such as *Erica carnea*, *Vaccinium myrtillus*, and *Vaccinium vitis-idaea*. Loose stands of Laricetum decidua on north facing slopes, where *Picea abies* and *Larix decidua* are torn out of the soil by powder avalanches, are typical for these moderately developed leptosols (Stöhr et al. 1995; Grabherr 1993; Mayer 1974).

Folic Leptosols, Folic Histosols

Most soil profiles from undisturbed forests near timberline show large accumulations of organic matter. These organic soils are often referred as “Tangelhumus”. The chemical properties of these organic layers are very much the same as those of morhumus on acidic rock. Bochter (1983) showed that mobile organic substances are precipitated in the O-C contact layers, similar to processes in “illuvial” spodic Bh-horizons of Podzols.

C/N ratios are wide (40 - 50) in the litter layer (OL) decreasing to 20 - 25 in the humus layer (OH). Although these organic layers have developed on calcareous rock, their pH-values are always very low (3 - 4), increasing sharply in the contact zone with the mineral soil or parent material.

Intensive browsing, reducing the forest cover may reduce the organic layer (Bochter et al. 1981) and the total amount of nutrients stored in the soil.

The understorey is dominated by acid tolerant dwarf shrubs such as *Rhododendron ferrugieum*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, and *Calluna vulgaris*. Forest cover consists mainly of *Pinus cembra* and *Larix decidua*, often with *Pinus mugo* in the understorey.

Chromic Cambisols

When layers of clay are present in the calcareous parent material, Chromic or Eutric Cambisols to Stagnic Gleysols may develop in poorly drained sinkholes (Glatzel 1999; Rehfuess 1990).

References

Aulitzky H (1963a) Die Bodentemperaturverhältnisse in der Kampfzone oberhalb der Waldgrenze und im subalpinen Zirben-Lärchenwald. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 153-208

Aulitzky H (1963b) Grundlagen und Anwendung des vorläufigen Wind-Schnee Ökogramms. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 60: 763-834

Bailly F, Nieder R (2001) Bezugsgrundlage der Bodenresourcen der Welt (WRB). In: Blume HP, Felix-Henningsen P, Fischer WR, Frede HG, Horn R, Stahr K (eds) Handbuch der Bodenkunde. Ecomed Verlag

Bednorz F (2000) Der Abbau der organischen Substanz im Waldgrenzökoton am Stillberg (Dischmatatal/Schweiz). Arbeiten aus dem Institut für Landschaftsökologie, Westfälische Wilhelms-Universität, Münster

Bochter R (1983) Böden naturnaher Bergwaldstandorte auf carbonatreichen Substraten. Nationalpark Berchtesgaden, Forschungsbericht 6

Bochter R, Neuerburg W, Zech W (1981) Humus und Humusschwund im Gebirge. Nationalpark Berchtesgaden, Forschungsberichte 2

Bortenschlager S (1984) Beiträge zur Vegetationsgeschichte Tirols I. Inneres Ötztal und unteres Inntal. Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck 71: 19-56

Bowmann W (1992) Inputs and storage of nitrogen in winter snow-pack in an alpine ecosystem. Arctic and Alpine Research 24: 211-215

Brooks PD, Williams MW (1999) Snow-pack controls on nitrogen cycling and export in seasonally snow covered catchments. Hydrological Processes 13: 2177-2190

Carcaillet C (2000) Changes in landscape structure in the northwestern Alps over the last 7000 years: lessons from soil charcoal. Journal of Vegetation Science 11: 705-714

Carcaillet C (2001) Are Holocene wood-charcoal fragments stratified in alpine and subalpine soils? Evidence from the Alps based on AMS 14C dates. The Holocene 11: 231–242

Carnelli AL, Theurillat JP, Thinon M, Vadi G, Talon B (2004) Past uppermost tree limit in the Central European Alps (Switzerland) based on soil and soil charcoal. The Holocene 14: 393-405

Fitze P (1980) Zur Bodenentwicklung auf Moränen in den Alpen. Geographica Helvetica 35: 97-112

Forstliche Bundesversuchsanstalt (1992) Österreichische Waldbodenzustandsinventur. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 168, Band I/II

Glatzel G, Hager H, Sieghardt M, Katzensteiner K, Ottner F, Wresowar M (1999) Waldböden und Bodenzustand in den Oberösterreichischen Kalkalpen. Institut für Waldökologie, Exkursion 1999 der Österreichischen Bodenkundlichen Gesellschaft, Eigenverlag

Grabherr G, Mucina L (1993) Die Pflanzengesellschaften Österreichs, Teil III, Wälder und Gebüsche. Gustav Fischer Verlag, Stuttgart

Gracanin Z (1972) Die Böden der Alpen. In: Ganssen R, Gracanin Z (eds) Bodengeographie. K.F. Koehler Verlag, Stuttgart, pp 172-195

Havranek WM (1972) Über die Bedeutung der Bodentemperatur für die Photosynthese und Transpiration junger Forstpflanzen und für die Stoffproduktion an der Waldgrenze. Angewandte Botanik 46: 101-116

Heikinnen O, Fogelberg B (1980) Bodenentwicklung im Hochgebirge: Ein Beispiel vom Vorfeld des Steingletschers in der Schweiz. Geographica Helvetica 35: 107-112

Helm D (1982) Multivariate analysis of alpine snow-patch vegetation cover near Milner Pass, Rocky Mountain National Park, Colorado, U.S.A. Arctic and Alpine Research 14: 87-95

Herman F, Smidt St, Englisch M, Jandl R (2004) Nitrogen flux studies in the North Tyrolean Limestone Alps. Forstliche Schriftenreihe, Universität für Bodenkultur, Wien 18: 157-171

Hiemstra CA, Reiners WA, Liston GE (2002) Spatial relationships between snow and ecosystem properties in a Wyoming alpine treeline ecotone: linking simulations and observations. Paper presented at the 70th Annual Meeting of the Western Snow Conference 2002: 1-10

Hiller B (2001) Humusformen im Waldgrenzökoton (Oberengadin, Schweiz). Arbeiten aus dem Institut für Landschaftsökologie, Westfälische Wilhelms Universität, Band 9

Holtmeier F-K (2003) Mountain timberlines. Ecology, patchiness, and dynamics. Advances in Global Change Research, vol 14. Kluwer Academic Publishers, Dordrecht, Boston, London

Jabiol B, Zanella A, Englisch M, Hager H, Katzensteiner K, Waal RW (2004) Towards a European classification of terrestrial humus forms. In: Institute of Soil Science and Forest Nutrition, University of Freiburg: EUROSOIL 2004, Sept. 4-12 2004, Freiburg, pp 1-10

Jenny H (1941) Factors of soil formation. McGraw-Hill, New York

Kneisel C, Hauck C, Von der Mühll D (2000) Permafrost below the timberline confirmed and characterized by geoelectric resistivity measurements, Bever Valley, Eastern Swiss Alps. Permafrost and Periglacial Processes 11: 295-304

Körner Ch (1999) Alpine plant life: functional plant ecology of high mountain ecosystems. Springer, Berlin, Heidelberg

Markart G, Kohl B, Sotier B, Schauer T, Bunza G, Stern R (2004) Provisorische Geländeanleitung zur Abschätzung des Oberflächenabflussbeiwertes auf alpinen Boden-/Vegetationseinheiten bei konvektiven Starkregen (Version 1.0). BFW-Dokumentation 3, Wien

Mayer H (1974) Wälder des Ostalpenraumes. Gustav Fischer Verlag, Stuttgart

Nestroy O (2002) Angleichung der österreichischen Bodennomenklaturen von 1969 und 2000 an die Europa Bodenkarte 1:1 Mio vom Jahre 1998. Mitteilungen der Österreichischen Bodenkundlichen Gesellschaft 65: 1-10

Neuwinger I (1965) Die Vegetations- und Bodenaufnahme als Beitrag zur Abgrenzung von Standortseinheiten. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 65: 129-158

Neuwinger-Raschendorfer I (1963) Bodenfeuchtemessungen. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 257-264

Neuwinger I, Czell A (1963) Böden in den Tiroler Zentralalpen. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 371-410

Newesely C, Tasser E, Spadinger P, Cernusca A (2000) Effects of land-use changes on snow gliding processes in alpine ecosystems. Basic and Applied Ecology 1: 61–67

Pauker SJ, Seastedt TR (1996) Effects of mobile tree islands on soil carbon storage in tundra ecosystems. Ecology 77: 2563–2567

Posch A (1980) Bodenkundliche Untersuchungen im Bereich der Glocknerstrasse in den Hohen Tauern. In: Franz H (ed) Untersuchungen an alpinen Böden in den Hohen Tauern 1974-1978 - Stoffdynamik und Wasserhaushalt. Veröffentlichungen des Österreichischen MaB-Hochgebirgsprogramms Hohe Tauern, vol 3. Universitätsverlag Wagner, Innsbruck, pp 90-107

Rehfuess KE (1990) Waldböden, Entwicklung, Eigenschaften und Nutzung. Pareys Studientexte 29. Verlag Paul Parey, Hamburg, Berlin

Reisigl H, Keller R (1987) Alpenpflanzen im Lebensraum. Alpine Rasen- Schutt- und Feldvegetation. Gustav Fischer Verlag, Stuttgart

Retzer JL (1974) Alpine soils. In: Ives JD, Barry RG (eds) Arctic and alpine environments. Methuen, London, pp 771-802

Sjögersten S (2003) Soil organic matter dynamics and methane fluxes at the forest-tundra ecotone in Fennoscandia. Comprehensive studies of Uppsala dissertations from the Faculty of Science and Technology 807

Smidt S (1996) Bewertung der Luftschadstoff- und Depositionsmeßergebnisse im Raum Achenkirch (1990-1995). In: Hermann F, Smidt S (eds) Ökosystemare Studien im Kalkalpin. FBVA Berichte 94, pp 157-174.

Stanton ML, Rejmanek M, Galen C (1994) Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito Range, Colorado, U.S.A. Arctic and Alpine Research 26: 364-374

Stöhr D, Aigner J, Aschaber R, Flaschberger J, Haselwandter G (19959 Naturschutzgebiet Karwendel – Biotopinventar/Naturpflegeplan 3: 1-15

Stottlemyer R, Rhoades C, Steltzer H (2001) Soil temperature, moisture, and carbon and nitrogen mineralization at a taiga-tundra ecotone, Noatak National Preserve, Northwestern Alaska. U.S. Geological Survey, Professional Paper 1678: 127-137.

Stumböck M (1999) Die spät- und postglaziale Vegetationsgeschichte des nordwestlichen Südtirols. Dissertationes Botanicae 299. Cramer, Berlin, Stuttgart

Tasser E, Mader M, Tappeiner U (2003) Effects of land use in alpine grasslands on the propability of landslides. Basic and Applied Ecology 4: 271-280

Tranquillini W (1979) Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. Ecological Studies, vol 31. Springer Berlin, Heidelberg, New York

Turner H (1961) Die Niederschlags- und Schneeverhältnisse. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 265-315

Van Husen D (1987) Die Ostalpen in den Eiszeiten. Populärwissenschaftliche Veröffentlichungen der Geologischen Bundesanstalt, Wien

Veit H, Mailänder R, Vonlanthen C (2002) Periglaziale Deckschichten im Alpenraum: bodenkundliche und landschaftsgeschichtliche Bedeutung. Petermanns Geographische Mittteilungen 146: 6-14

Wick L, Van Leeuwenl JFN, Van der Knaap WO, Lotter1 AF (2003) Holocene vegetation development in the catchment of Sägistalsee (1935 m asl), a small lake in the Swiss Alps. Journal of Paleolimnology 30: 261–272

4 Mycorrhiza in the Alpine Timberline Ecotone: Nutritional Implications

Kurt Haselwandter

Institut für Mikrobiologie, Universität Innsbruck

4.1 Introduction

In the alpine-treeline ecotone soil moisture levels are high with decomposition and mineralization processes inhibited as a result of low soil temperatures, high rain- or snowfall and low evaporation rates. Under these circumstances, organic matter accumulates to give deposits of peat or mor-humus. Hence, important nutrients including e.g. nitrogen become immobilized, thus rendering them unavailable for plant nutrition (cf. Chap. 3).

Under such circumstances, the role mycorrhizal fungi play with regard to nutrient supply to the associated host plants becomes crucial (Smith and Read 1997). Nutrient uptake by the uninfected root is closely related to rooting intensity and the volume of soil from which nutrients are extracted by the roots and root hairs. That leaves considerable volumes of soil between the roots which are not being used. The outgrowth of hyphae of mycorrhizal fungi into soil far beyond the root or root hair zone considerably increases the volume of soil tapped for nutrients. The fungal hyphae absorb and translocate essential nutrients into the root (Haselwandter and Bowen 1996). In addition, and most likely of particular importance in a situation where the nutrients are locked up in organic matter like in the soils of the alpine-treeline ecotone, the hyphal network of mycorrhizal fungi may provide access to organically bound nutrients which otherwise would not be available for support of plant growth. Thus the mycorrhizal fungi do not only dramatically enlarge the surface area of the root system through which nutrients can be absorbed, they also bring into the system

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additional biochemical capacities an uninfected plant root is completely lacking.

4.2 Mycorrhizal symbioses in the alpine-treeline ecotone

In the temperate zone, forests are dominated by tree species forming the ectomycorrhizal symbiosis. The tree species of the alpine timberline and treeline are exclusively ectomycorrhizal (Moser 1967; Trappe and Fogel 1977). At the alpine tree line the most abundant tree species are *Picea abies, Larix decidua* and *Pinus cembra*. The following basidiomycota are typically associated: With *L. decidua* the basidiomycota *Suillus grevillei*, *S. tridentinus, S. viscidus*, *Boletinus cavipes, Lactarius porninsis, Hygrophorus lucorum*, and with *P. cembra* the basidiomycota *S. plorans, S. placidus, S. sibiricus, Chroogomphus helveticus*, respectively (Moser 1963; nomenclature follows Horak 2005). According to Moser (1982) a great number of EM fungal species (including dominant taxa) of the alpine timberline were never observed in the 'kampfzone' which extends from the alpine timberline to the treeline. Hence, major differences between EM fungal communities might exist along an altitudinal gradient, and environmental conditions may limit the distribution of EM fungal taxa. This might be independent of the distribution of their host plants, or caused by a combination of environmental factors and patterns of host plant distribution (Gardes and Dahlberg 1996). An elevation dependent decrease in richness and diversity of ectomycorrhizal fungi was observed also in the Front Range of the Canadian Rockies, likely governed by host plant distribution and edaphic factors (Kernaghan and Harper 2001).

Although in the past sporocarp surveys may have provided some useful information on ectomycorrhizal fungal diversity, most recently the use of molecular approaches has dramatically increased our knowledge on the diversity of EM fungal communities present in different ecosystems (Horton 2002). It has become clear that there is a mismatch between fungi that appear dominant as sporocarps and those that appear dominant on EM roots. EM fungal communities are strikingly divers and patchily distributed at a fine scale (Horton and Bruns 2001). Unfortunately detailed studies employing the modern methodology in studies focusing on the alpine-treeline ecotone are still missing, albeit desperately needed.

In the alpine-treeline ecotone the understorey is dominated by ericaceous plant species like *Rhododendron ferrugineum, R. hirsutum, Vaccinium myrtillus, V. vitis-idaea, V. uliginosum*, all of which forming typical ericoid mycorrhizas (Haselwandter 1987). Pure cultures of fungi isolated from ericoid roots and confirmed in re-synthesis experiments usually remain sterile. The first taxon to be recognized as typical ericoid mycorrhizal fungus was the ascomycete *Hymenoscyphus ericae* forming e.g. the ericoid mycorrhizae of *Calluna vulgaris*, with its anamorph *Scytalidium vaccinii* (Egger and Sigler 1993; Read 1996). Apothecium production was also induced in a pure culture isolated from *Ledum groenlandicum* confirming that *H. ericae* and *S. vaccinii* are states of a single species (Hambleton et al. 1999). It is interesting to note that also ectomycorrhizae may be formed by a telemorph and mitosporic anamorph belonging to the same fungal species, e.g. within the genus *Tuber* (Urban et al. 2004). On the basis of morphological, ecological, and molecular characteristics the *H. ericae* aggregate is now placed in the newly established genus *Rhizoscyphus* as *R. ericae* (Zhang and Zhuang 2004).

Other anamorphic ericoid mycorrhizal fungi are *Oidiodendron* spp. with their telemorphs in the ascomycetous Helotiales (Gibas et al. 2002), formerly included in the Onygenales (Perotto et al. 2002). Of the two most frequently isolated fungi either *H. ericae* or *O. maius* seems to dominate in a given habitat. While *Calluna vulgaris* from two mine sites and an uncontaminated natural heathland in southwest England was mainly colonized by *H. ericae* (Sharples et al. 2000), in northern Italy *Oidiodendron maius* was the most prominent mycorrhizal fungus of the same plant species (Perotto et al. 1996).

Bergero et al. (2000) have demonstrated that *Oidiodendron* spp. and some sterile fungal morphotypes may be associated with ericoid and ectomycorrhizal plants. *In vitro*, fungal isolates of *Quercus ilex* formed ericoid mycorrhizae with *Erica arborea* (Bergero et al. 2000). According to molecular data some of these isolates were conspecific with mycorrhizal endophytes naturally infecting *E. arborea* roots. It is interesting to note, that in such roots also hyphae with clamp connections and dolipore septa were observed, albeit unculturable yet. Also most *Gaultheria shallon* root segments were shown to contain an unculturable basidiomycete as revealed by PCR amplification, cloning and sequencing of LSU (large-subunit) fungal DNA (Berch et al. 2002).

Molecular data suggest that ericoid mycorrhizal fungi may cover a wider spectrum of taxa than previously thought, most of them unidentified so far. Ribosomal DNA sequence analysis revealed that the ectomycorrhizal fungal symbiont of *Piceirhiza bicolorata* shared about 95% ITS1 (internal transcribed spacer) sequence identity with *H. ericae* aggregate (Vralstad et al. 2000). In re-synthesis experiments three out of nine *H. ericae* aggregate strains of ectomycorrhizal origin formed ectomycorhizae with *Picea abies*, *Pinus sylvestris* and *Betula pubescens*, but none of the ectomycorrhiza forming isolates produced ericoid mycorrhizae on *Vaccinium* *vitis-idaea* On the other hand, the *H. ericae* strains of ericoid origin formed ericoid mycorrhizae with *V. vitis-idaea*, but none of the three isolates tested produced ectomycorrhizae on *P. abies*, *P. sylvestris* and *B. pubescens* as potential ectomycorrhizal hosts (Vralstad et al. 2002). Only recently, one fungal isolate from the *H. ericae* aggregate obtained from *Piceirhiza bicolorata*-like ectomycorrhizas was shown to form both, ectomycorrhizas with *P. sylvestris* seedlings and hyphal coils in *V myrtillus* roots, characteristic of ericoid mycorrhizas (Villarreal-Ruiz et al. 2004).

Thus it may appear possible that ericaceous shrubs and non-ericaceous trees may share some symbionts. However, when ectomycorrhizal trees like spruce are planted into heathland dominated by plants colonized by fungi of the *H. ericae* type, the conifer roots normally not only do not produce the *P. bicolorata* morphotype, but instead may be attacked by pathogenic fungi (Read 2000). Furthermore, at high elevation the success rate of afforestation with *Pinus cembra* in the alpine dwarf shrub heath dominated by ericoid mycorrhizae usually increases when the seedlings are inoculated with appropriate ectomycorrhizal basidiomycetes in the nursery (Moser 1964). Hence despite some possible genotypic overlaps between mycorrhizal partners as revealed through molecular analysis of fungal biodiversity detectable in plant roots, this does not necessarily mean that the genetic diversity is reflected by the functional diversity displayed by the respective mycorrhizal fungi in the ecosystem, at least not until sound experiments have been carried out and provided proof (Read 2000).

In that connection, it has to be mentioned that a substantial proportion of ectomycorrhizal *Pseudotsuga* seedlings may be colonized by basidiomycetous fungi that were also associated with the ericaceous plant *Arctostaphylos* forming arbutoid mycorrhizae (Horton et al. 1999). This study also indicated that these fungal root associates contribute to the establishment of *Pseudotsuga* seedlings.

4.3 Nutritional aspects with special reference to organic nitrogen

Mineral and organic fertilizers can significantly improve plant growth and tree vigour as was shown in reforestation and revitalization experiments carried out in the Alps at 1750 m a.s.l. in an area where the timberline is at an elevation of 2000 m a.s.l. (Glatzel et al. 1991). In general, low availability of N is limiting the productivity of boreal and temperate forests in the northern hemisphere, at least at the timberline. It is therefore of great interest to compare the possible role of ectomycorrhizal and ericoid mycorrhizal fungi in the N turnover in such ecosystems and their potential contribution to the N nutrition of the respective host plants. Special emphasis must be laid upon their role in the mobilization of organically bound N as in the alpine-treeline ecotone this is the predominant form of N source.

In microcosm studies addition of patches of organic matter was shown to lead to proliferation of ectomycorrhizal mycelium in the organic matter. In such patches increased activities of hydrolyzing enzymes necessary for nutrient mobilization were observed and significant amounts of N, P and K were removed from such patches by the ectomycorrhizal fungal mycelia (Bending and Read 1995a, b). Nutrient mobilization from natural organic substrates present in the fermentation horizon of forest soils may be a key function of the vegetative mycelium of ectomycorrhizal plants (Perez-Moreno and Read 2000). However, saprotrophic fungi may be superior in removing nutrients from litter (Colpaert and van Tichelen 1996) suggesting that ectomycorrhizal fungi preferentially forage in patches of substrate which are already decomposed to some extent (Olsson et al. 2002). Nevertheless, it is assumed that uptake of organic nutrients by ectomycorrhizal fungi is of significance for ectomycorrhizal trees, possibly leading to a short-circuiting of the nitrogen cycle as suggested by Leake et al. (2002).

This represents an analogy with the ericoid mycorrhizal system. Especially in the acid soils of the alpine dwarf shrub heath net mineralization rates are low. Rehder and Schäfer (1978) have already indicated that the plant uptake of N could not be accounted for by such mineralization processes, and have therefore suggested an additional and direct uptake of N through mycorrhizal fungi supporting the growth of ericaceous plants. Various simple and complex organic forms of N and P are readily assimilated by ericoid mycorrhizal fungi, and in symbiosis, the transfer to the host plants of nutrients originally contained in polymers is facilitated by the fungal hyphae. This is a feature of this specific mycorrhizal association which contributes significantly to the ability of ericaceous plants to grow on soils with high organic matter content which are extremely poor in readily available nutrients (Smith and Read 1997).

In the alpine-treeline ecotone soils extraradical mycelia of different kinds of mycorrhiza are intermingled, predominantly representing ectomycorrhizal and ericoid mycorrhizal hyphae. Each of the populations of symbiotic soil fungi is endowed with biochemical and physiological capacities, at least some of which displaying some features which they may have in common as outlined above. Such a notion makes it necessary to discuss whether the two dominant mycorrhiza forms tap the same or different soil nutrient pools from which they transfer e.g. N to the associated host plants. By the use of the δ^{15}N technique Schulze et al. (1994) have shown that at the northern treeline of Alaska with an ericaceous understory ectomycorrhizal tree species like *Picea glauca* and *P. mariana* are tapping other nutrient pools (N) than the ericoid mycorrhizal dwarf shrub *Vaccinium vitis-idaea* or the arbuscular mycorrhizal grass *Calamagrostis canadensis*. A wide range of N compounds may be used for the N nutrition of plants growing in a boreal forest, and the type of mycorrhizal symbiosis may be of great importance for scavenging of immobilized N from soil (Persson et al. 2003). Different mycorrhiza types can tap different sources of soil nutrients (Aerts 2002).

On the other hand, in the alpine-treeline ecotone trees may share the same mycorrhizal fungal partner with ericaceous dwarf shrubs as outlined above. Under such circumstances the trees as well as the ericaceous understorey can be assumed to have access to the same nutrient (N) pool through the biochemical features displayed by the identical mycorrhizal fungal associates. Hence the question arises whether host specific factors determine which nutrients are tapped at what time from the same pool, and translocated to the respective host plant. Different source-sink relationships may govern the nutrient transfer from soil into plant through the hyphae of the mycorrhizal fungi associated with individuals of both, tree species as well as ericaceous dwarf shrub species.

4.4 Concluding remarks

Ericoid and ectomycorrhizal fungi may be directly involved in the degradation of detrital materials of microbial, faunal and plant origins, which leads to the mobilization of N and P from organic polymers in which they are sequestered in soil (Read and Perez-Moreno 2003). There is no doubt that in general N is the most important growth limiting nutrient. However, in case the N supply reaches a level high enough for supporting plant growth, another nutrient like P may become growth limiting. So the demand for nutrients ought to be considered dynamic rather than static and fixed at a certain level. In that respect the extensive extraradical fungal mycelium of the alpine-treeline ecotone plants may adopt an important buffering role and become a sort of nutrient reservoir from which nutrients may be obtained upon demand, possibly controlled also by source-sink relationships.

Due to the high organic matter content of alpine-treeline ecotone soils a nutrient like iron may achieve ecological and plant nutritional significance. It was shown that the rhizosphere of ectomycorrhizal pine and spruce contained higher hydroxamate siderophore concentrations than surrounding bulk soil (Reid et al. 1984). Recently, the structure of the main siderophore released by the wide spread ectomycorrhizal fungus *Cenococcum geophilum* was elucidated and identified as the cyclic hexapeptide ferricrocin (Haselwandter and Winkelmann 2002). Interestingly, also typical ericoid mycorrhizal fungi of acid soils like *Hymenoscyphus ericae* and *Oidiodendron griseum* release ferricrocin as main siderophore (Haselwandter et al. 1992). It is possible that the biosynthesis of ferricrocin by different mycorrhizal fungi may be differently regulated by factors like iron availability and pH in the environment. Such ferric iron scavenging compounds were shown to have implications for the iron nutrition of host plants (cf. Haselwandter 1995). Furthermore, microbial siderophores together with low molecular weight organic acids are considered important for weathering processes leading to dissolution of rock material (Hoffland et al. 2004).

At high elevation sites characterised by abiotic extremes facilitative interactions between plants appear to be more important than competitive interactions (Callaway 1998). There are indications that a below-ground mechanism involving ectomycorrhizas may mediate tree facilitation of seedlings at the alpine treeline (Hasselquist et al. 2005). Undoubtedly, soil microorganisms including mycorrhizal fungi play important roles in the alpine-treeline ecotone. That means, whenever any measures have to be taken for e.g. revitalization of protective forests in the Alps, their effects upon these soil micro-organisms have to be assessed, preferentially in long-term observations and experiments.

References

Aerts R (2002) The role of various types of mycorrhizal fungi in nutrient cycling and plant competition. In: Van der Heijden MGA, Sanders IR (eds) Mycorrhizal ecology. Springer, Berlin, pp 117- 133

Bending GD, Read DJ (1995a) The structure and function of the vegetative mycelium of ectomycorrhizal plants. V. The foraging behaviour of ectomycorrhizal mycelium and the translocation of nutrients from exploited organic matter. New Phytologist 130: 401-409

Bending GD, Read DJ (1995b) The structure and function of the vegetative mycelium of ectomycorrhizal plants. VI. Activities of nutrient mobilising enzymes in birch litter colonised by *Paxillus involutus* (Fr.) Fr. New Phytologist 130: 411-417

Berch SM, Allen TR, Berbee ML (2002) Molecular detection, community structure and phylogeny of ericoid mycorrhizal fungi. Plant and Soil 244: 55-66

Bergero R, Perotto S, Girlanda M, Vidano G, Luppi AM (2000) Ericoid mycorrhizal fungi are common root associates of a Mediterranean ectomycorrhizal plant (*Quercus ilex*). Molecular Ecology 9: 1639-1650

Callaway RM (1998) Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. Oikos 82: 561-573

Colpaert JV, van Tichelen KK (1996) Decomposition, nitrogen and phosphorus mineralization from beech leaf litter colonized by ectomycorrhizal or litter-decomposing basidiomycetes. New Phytologist 134: 123-132

Egger KN, Sigler L (1993) Relatedness of the ericoid endophytes *Scytalidium vaccinii* and *Hymenoscyphus ericae* inferred from analysis of ribosomal DNA. Mycologia 85: 219-230

Gardes M, Dahlberg A (1996) Mycorrhizal diversity in arctic and alpine tundra: an open question. New Phytologist 133: 147-157

Gibas CFC, Sigler L, Summerbell RC, Currah RS (2002) Phylogeny of the genus *Arachnomyces* and its anamorphs and the establishment of *Arachnomycetales*, a new eurotiomycete order in the *Ascomycota*. Studies in Mycology 47: 131-139

Glatzel G, Haselwandter K, Katzensteiner K, Sterba H, Weissbacher J (1991) The use of organic and mineral fertilizers in reforestation and in revitalization of declining protective forests in the Alps. Water, Air, and Soil Pollution 54: 567-576

Hambleton S, Huhtinen S, Currah RS (1999) *Hymenoscyphus ericae*: A new record from western Canada. Mycological Research 103: 1391-1397

Haselwandter K (1987) Mycorrhizal infection and its possible ecological significance in climatically and nutritionally stressed alpine plant communities. Angewandte Botanik 61: 107-114

Haselwandter K (1995) Mycorrhizal fungi: Siderophore production. Critical Review of Biotechnology 15: 287-291

Haselwandter K, Bowen GD (1996) Mycorrhizal relations in trees for agroforestry and land rehabilitation. Forest Ecology and Management 81: 1-17

Haselwandter K, Winkelmann G (2002) Ferricrocin – an ectomycorrhizal siderophore of *Cenococcum geophilum*. BioMetals 15: 73-77

Haselwandter K, Dobernigg B, Beck W, Jung G, Cansier A, Winkelmann G (1992) Isolation and identification of hydroxamate siderophores of ericoid mycorrhizal fungi. BioMetals 5: 51-56

Hasselquist N, Germino MJ, McGonigle T, Smith WK (2005) Variability of *Cenococcum* colonization and its ecophysiological significance for young conifers at alpine-treeline. New Phytologist 165: 867-873

Hoffland E, Kuyper TW, Wallander H, Plassard C, Gorbushina AA, Haselwandter K, Holmström S, Landeweert R, Lundström US, Rosling A, Sen R, Smits MM, van Hees AW, van Breemen N (2004) The role of fungi in weathering. Frontiers in Ecology and the Environment 2: 258-264

Horak E (2005) Röhrlinge und Blätterpilze in Europa. Spektrum, Akademischer Verlag / Elsevier, München. 6. Auflage

Horton TR (2002) Molecular approaches to ectomycorrhizal diversity studies: variation in ITS at a local scale. Plant and Soil 244: 29-39

Horton TR, Bruns TD 2001. The molecular revolution in ectomycorrhizal ecology: peeking into the black-box. Molecular Ecology 10: 1855-1871

Horton TR, Bruns, TD, Parker VT (1999) Ectomycorrhizal fungi associated with *Arctostaphylos* contribute to *Pseudotsuga* establishment. Canadian Journal of Botany 77: 93-102

Kernaghan G, Harper KA (2001) Community structure of ectomycorrhizal fungi across an alpine/subalpine ecotone. Ecography 24: 181-188

Leake JR, Donnelly DP, Boddy L (2002) Interactions between ecto-mycorrhizal fungi and saprotrophic fungi. In: Van der Heijden MGA, Sanders IR (eds) Mycorrhizal ecology. Springer, Berlin, pp 345-372

Moser M (1963) Förderung der Mykorrhizabildung in der forstlichen Praxis. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 60: 691-720

Moser M (1964) Die Mykorrhizafrage bei der Anzucht von Forstpflanzen für das Hochgebirge. In: Forstsamengewinnung und Pflanzenanzucht für das Hochgebirge. BLV Verlagsgesellschaft München, Basel, Wien, pp 225-231

Moser M (1967) Die ektotrophe Ernährungsweise an der Waldgrenze. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 75: 357-380

Moser M (1982) Mycoflora of the transitional zone from subalpine forests to alpine tundra. In: Laursen GA, Ammirati JF (eds) Arctic and Alpine mycology, vol 1. Seattle: University of Washington Press, pp 371-384

Olsson PA, Jakobsen I, Wallander H (2002) Foraging and resource allocation strategies of mycorrhizal fungi in a patchy environment. In: Van der Heijden MGA, Sanders IR (eds) Mycorrhizal ecology. Springer, Berlin, pp 93-115.

Perez-Moreno J, Read DJ (2000) Mobilization and transfer of nutrients from litter to tree seedlings via the vegetative mycelium of ectomycorrhizal plants. New Phytologist 145: 301-309

Perotto S, Actis-Perino E, Perugini J, Bonfante P (1996) Molecular diversity of fungi from ericoid mycorrhizal roots. Molecular Ecology 5: 123-131

Perotto S, Girlanda M, Martino E (2002) Ericoid mycorrhizal fungi: some new perspectives on old acquaintances. Plant and Soil 244: 41-53

Persson J, Högberg P, Ekblad A, Högberg MN, Nordgren A, Näsholm T (2003) Nitrogen acquisition from inorganic and organic sources by boreal forest plants in the field. Oecologia 137: 252-257

Read DJ (1996) The structure and function of the ericoid mycorrhizal root. Annals of Botany 77: 365-374

Read DJ (2000) Links between genetic and functional diversity – a bridge too far? New Phytologist 145: 363-365

Read DJ, Perez-Moreno J (2003) Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? New Phytologist 157: 475-492

Rehder H, Schäfer A (1978) Nutrient turnover studies in alpine ecosystems. IV. Communities of the Central Alps and comparative survey. Oecologia 34: 309-327

Reid RK, Reid CPP, Powell PE, Szansiszlo JP (1984) Comparison of siderophore concentrations in aqueous extracts of rhizosphere and adjacent bulk soils. Pedobiologie 26: 263-266

Schulze E-D, Chapin FS III, Gebauer G (1994) Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. Oecologia 100: 406-412

Sharples JM, Chambers SM, Mehrag AA, Cairney JWG (2000) Genetic diversity of root-associated fungal endophytes from *Calluna vulgaris* at contrasting field sites. New Phytologist 148: 153-162

Smith SE, Read DJ (1997) Mycorrhizal symbiosis, 2nd edn. Academic Press, San Diego

Trappe JM, Fogel RD (1977) Ecosystematic functions of mycorrhizae. In: The Belowground ecosystem: a synthesis of plant-associated processes. Range Sci. Dep. Sci. Ser. No. 26, Colorado State University, Fort Collins, pp 205-214

Urban A, Neuner-Plattner I, Krisai-Greilhuber I, Haselwandter K (2004) Molecular studies on terricolous microfungi reveal novel anamorphs of two *Tuber* species. Mycological Research 108: 749-758

Villarreal-Ruiz L, Anderson IC, Alexander IJ (2004) Interaction between an isolate from the *Hymenoscyphus ericae* aggregate and roots of *Pinus* and *Vaccinium*. New Phytologist 164: 183-192

Vralstad T, Fossheim T, Schumacher T (2000) *Piceirhiza bicolorata* – the ectomycorrhizal expression of the *Hymenoscyphus ericae* aggregate ? New Phytologist 145: 549-563

Vralstad T, Schumacher T, Taylor AFS (2002) Mycorrhizal synthesis between fungal strains of the *Hymenoscyphus ericae* aggregate and potential ectomycorrhizal and ericoid hosts. New Phytologist 153: 143-152

Zhang Y-H, Zhuang W-Y (2004) Phylogenetic relationships of some members in the genus *Hymenoscyphus* (Ascomycetes, Helotiales). Nova Hedwigia 78: 475-484

5 Vegetation at the Upper Timberline

Brigitta Erschbamer and Susanne Wallnöfer

Institut für Botanik, Universität Innsbruck

5.1 Introduction

The upper timberline is one of the most fascinating vegetation boundaries in the Alps (Reisigl and Keller 1989) and in the mountain ecosystems of the world in general. Depending on the environmental conditions such as climate (oceanic External Alps vs. continental Inner Alps) or geology (limestone vs. silicate), different woody species may occur at the upper timberline in the European Alps. The boreal conifers *Picea abies, Larix decidua, Pinus cembra, Pinus uncinata,* and *Pinus mugo* are highly frost resistant (resistance down to –70 °C, Sakai and Larcher 1987; see also Chap. 10), thus they are the most widespread alpine timberline species. Other conifers such as *Abies alba, Pinus sylvestris* and deciduous trees such as *Fagus sylvatica* and *Acer pseudoplatanus* with lower frost resistance can reach the timberline only in the oceanically influenced External Alps where milder winter climate predominates. Among the shrubs few deciduous species reach the high-altitudinal coniferous forests: *Sorbus aucuparia*, *Sorbus chamaemespilus*, *Lonicera coerulea.* In addition, *Betula pendula* and *Populus tremula* occur as pioneer species up to the limit of the forests. The shrub *Alnus alnobetula* (syn. *A. viridis)* pre-dominates the azonal vegetation on slopes along running water or in avalanche paths, or forms secondary communities on abandoned moist pastures at the timberline.

G. Wieser and M. Tausz (eds.), Trees at their Upper Limit, 67–78.

5.2 Growth forms at the timberline

The forests close to the timberline have a lower canopy density and the trees grow to a smaller height. A considerable change of the growth form is significant with increasing altitude (see Chap. 1). Conifers show already in the high-montane belt a typical columnar form with acute crowns. Steep slopes, snow pressure and wind are responsible for stem deformations causing sabre (bow) or harp forms, flags, scrubs or knee forms (Schönenberger 1981; Holtmeier 2003). Most tree species spread their branches down to the ground (e.g. *Fagus sylvatica*, Fanta 1981). Timber atolls (= tree groups, Tranquillini 1979) formed by *Picea abies* or *Larix decidua* are characteristic for the timberline ecotone. According to Kuoch and Amiet (1970) such atolls are a special form of vegetative propagation by layering. On branches covered by litter and humus adventitious roots are formed and the distal part of the branches becomes an erect tree.

5.3 Plant communities at the timberline

A natural timberline can be observed only in very few places of the Alps (Mayer 1974; Tranquillini 1979; Ellenberg 1996). *Pinus cembra*, for instance, is able to build a closed forest up to the limit of tree growth, forming a sharp timberline (Tranquillini 1979). In general, however, due to anthropogenic impacts a scattered timberline with a broad transition zone ("*Kampfzone*"; cf. Chap. 1) can be found above the closed forest, forming a mosaic of forest-, dwarf shrub heath- and grassland patches. Palynological records confirm the anthropogenic impact for thousands of years (Bortenschlager 1993). Burning of high-altitude forests has been recorded already since the neolithic period (Patzelt et al. 1997) and then - more enhanced - since the bronze-age (Neuwinger 1970; Patzelt et al. 1997, see also Chap. 3).

Due to massive impacts and clearings during the middle age, the timberline was lowered by 200-400 m (Friedel 1967; Breitenmoser 1998). Today, several anthropo-zoogenic communities extend on the potential forest sites at the timberline (communities of the classes Loiseleurio-Vaccinietea, Molinio-Arrhenatheretea, Caricetea curvulae, Seslerietea variae) forming a mosaic of forest relicts with open grassland patches and dwarf shrubs. Recently, land abandonment and changes in agroforestry have caused a significant change below and at the timberline zone, thus the area of forests has been increasing during the last decades and extending on formerly deforested sites (Brändli 2000; Bätzing 2003). However, the secondary succession towards a forest seems to depend highly on the type of the anthropo-zoogenic community. In the Swiss National Park for instance, succession models predict 515 to 630 years for tall-herb communities to be replaced by pine forests (Schütz et al. 2000). In general, forest regeneration seems to fail on areas where a forest would be highly desired for protection against avalanches, land slides and erosion (Bätzing 2003).

In the following the most important plant communities at the timberline will be described.

5.3.1 Spruce forests (*Picea abies* communities)

Among the forest communities occurring up to the timberline the so-called ”subalpine” spruce forests are the most widespread ones. They are less dense compared to montane spruce forests and the trees are typically columnar with acute crown forms. At the timberline *Picea* is generally intermingled with *Pinus uncinata* (W-Alps) or *Pinus mugo* (E-Alps), both species colonizing the shallow rocky sites (Ozenda 1988).

Subalpine spruce forests are widely distributed in the Inner and Intermediate Alps, occurring at 1600 - 1900 m a.s.l.. In the External Alps they occur up to 1800 m a.s.l. In the northern External Alps subalpine *Picea abies* forests are common from Dauphiné to the eastern end of the Alps. In the southern External Alps they become increasingly rare in the W, e.g. in Switzerland (Ott et al. 1997). In the SW-Alps *Picea abies* is largely missing.

More or less similar subalpine spruce forest types were described in the E-and W-Alps (Wallnöfer 1993a; Ott et al. 1997; Ewald 1999). Subalpine spruce forests on silicate (Homogyno-Piceetum, Larici-Piceetum) are widespread, e.g. in the central chains of the E-Alps, in the Swiss National Park, Tarentaise, Alps de Savoie and relictic also in the French S-Alps (Mayer 1986). *Pinus cembra* and *Larix decidua* can be present in the tree layer. The understorey is rich in mosses, dwarf shrubs (*Vaccinium myrtillus*) and grasses (*Calamagrostis villosa*).

On moist, nutrient-rich soils in shadowy locations spruce forests with tall forbs (Adenostylo alliariae-Piceetum) are characteristically developed in the subalpine belt. They occur both in the E- and W-Alps (Ellenberg and Klötzli 1972; Zukrigl 1973; Frey 1995).

On substrates rich in carbonate a distinct species-rich type can be found (Adenostylo glabrae-Piceetum, Calamagrostio variae-Piceetum, Wallnöfer 1993a; Ott et al. 1997). *Larix decidua* occurs regularly in the tree layer, occasionally also *Acer pseudoplatanus* and *Abies alba*. In the Julic Alps the understorey of this forest type is enriched by illyric elements (Mayer 1986).

On dry, shallow limestone and dolomite slopes an open spruce forest type with *Acer pseudoplatanus, Sorbus aria* and *S. aucuparia* is typical for the Northern Calcareous Alps (Carici albae-Piceetum, Wallnöfer 1993a) and in the Swiss Alps (Polygalo chamaebuxi-Piceetum, Ott et al. 1997).

5.3.2 Fir forests (*Abies alba* communities)

In general the main distribution of *Abies alba* lies in the montane belt of the External and Intermediate Alps, while it occurs only sporadically in subalpine forests. An exception are subalpine fir forests in the southern W-Alps where *Picea abies* is rare or absent (Mercantour, Argentera, Liguric Alps, Alps of Ticino). The community called Rhododendro ferruginei-Abietetum can be found on north-facing slopes on siliceous bedrock at 1550 - 1900 m a.s.l. (Kuoch 1954; Barbero et al. 1970; Ott et al. 1997). It is characterized by a high frequency of *Larix decidua* in the tree layer and by *Rhododendron ferrugineum* in the understorey. The Rhododendro-Abietetum is often situated in close contact with subalpine larch forests (Kuoch and Amiet 1970).

5.3.3 Larch-Swiss stone pine forests (*Larix decidua-Pinus cembra* communities)

In the Inner Alps and partly also in the Intermediate Alps a Larici-Pinetum cembrae forms an upper subalpine forest belt between subalpine spruce forests and the timberline. In addition in some parts of the northern External Alps spatially limited *Pinus cembra* forests exist (Ott et al. 1997; Walentowski et al. 2004). In the French W-Alps (Dauphiné) the Larici-Pinetum cembrae reaches 2500 m a.s.l., in the Swiss Alps 2400 m, in the central chains of the E-Alps 2300 m, in eastern chains 2000 m a.s.l. In protected niches *Pinus cembra* is able to grow also up to 2700 m a.s.l. (Monviso-area, Italy, Hofmann 1970).

The most widespread larch-Swiss stone pine community is the Larici-Pinetum cembrae on siliceous soils. Larch may be completely absent, whereas spruce may occur sporadically. The understorey is rather similar to that of subalpine spruce forest on silicate: either rich in mosses and grasses (*Avenella flexuosa, Calamagrostis villosa, Luzula* spp.) or dominated by dwarf shrubs (*Vaccinium* spp., *Juniperus communis* ssp. *alpina*). Anthropo-zoogenically influenced forests show openings and they are dominated by *Rhododendron ferrugineum* or *Calamagrostis villosa.*

On south-facing rocky slopes on silicate in the W-Alps a xerophilous type of the Larici-Pinetum cembrae with *Juniperus communis* ssp. *alpina, Cotoneaster integerrimus* and *Arctostaphylos uva-ursi* was described (Cotoneastro-Pinetum cembrae; Béguin and Theurillat 1982; Ozenda 1988).

On calcareous bedrock (e.g. Calcareous Alps of Salzburg, Dolomites) another type of the Larici-Pinetum cembrae with high frequency of larch can be found (Mayer 1974; Oberdorfer 1992). *Sorbus chamaemespilus* and *Lonicera coerulea* form the shrub layer. All the three *Rhododendron* species (*Rh. hirsutum, Rh. ferrugineum, Rh. intermedium*) may be present. Also tall forbs (eventually on moist slopes even *Alnus alnobetula*) or *Pinus mugo, Rhodothamnus chamaecistus* may appear.

A xerophilous type on carbonate with *Erica carnea* and *Sesleria albicans* in the understorey was described in the Italian Alps (Odasso 2002) and in the Swiss Alps (Frehner et al. 2005).

5.3.4 Larch forests (*Larix decidua* communities)

Larix decidua is frequently encountered in various subalpine forest communities, such as the Larici-Pinetum cembrae (Mayer 1962). It often occurs as a pioneer species. Beyond the distribution area of *Pinus cembra* pure larch forests are predominating in the subalpine belt of the SW-Alps (Barbero et al. 1970; Ozenda 1988). A frequent though partly anthropogenic community is the Junipero-Laricetum. It is an open forest on sunny and dry siliceous slopes with *Juniperus communis* ssp. *alpina, Vaccinium myrtillus, Calamagrostis villosa* in the understorey (Frehner et al. 2005).

In other parts of the Alps less extensive larch communities mostly on rocky substrate or on bolder were described. In the NE- and SE-Alps on limestone and dolomite larch forests dominated by *Rhododendron hirsutum* and/or *Rhodothamnus chamaecistus* were recorded (Zukrigl 1973).

On shallow south-exposed slopes on silicate the Junipero sabinae-Laricetum occurs in the Austrian Inner Alps (with *Juniperus sabina*, *J. communis* ssp. *alpina, Calamagrostis varia*; Wallnöfer 1993b).

A subalpine Adenostylo alliariae-Laricetum rich in tall forbs can be found in the Inner Alps of Switzerland (Ott et al. 1997).

5.3.5 *Pinus uncinata* forests

In the W-Alps *Pinus uncinata* forests substitute the subalpine *Picea abies* communities and the Larici-Pinetum cembrae on extremely shallow soils on calcareous and dolomitic sites, less frequently on silicate. The distribution area of *Pinus uncinata* extends from the Sea Alps to the Fernpass and Ofenpass, respectively. It is a low-demanding species regarding the supply of nutrients and water (Kuoch and Schweingruber 1975). *Pinus uncinata* forests can be found both in the external mountain ranges and in the inner mountain chains (Schweingruber 1972; Ozenda 1988; Frey 1995). In the Swiss National Park (Graubünden) *Pinus uncinata* forests are covering large areas (Braun-Blanquet et al. 1954). In part they can be considered as a pioneer stage after clearings (Mayer 1974).

Frequently, *Pinus uncinata* can be found in close contact with subalpine spruce forest forming an environmental catena from shallow nutrient-poor soils to well developed soils where spruce predominates. Similar to the *Pinus mugo* scrubs, the description of the communities results according to the dominance of different dwarf shrubs – *Erica carnea*, *Rhododendron hirsutum* and *Rh. ferrugineum*, *Juniperus communis* ssp. *alpina* and *Arctostaphylos uva-ursi* (for instance Erico carneae-Pinetum uncinatae, Mayer 1986). Badly-growing spruce and larch can be mixed in. In the Swiss National Park, *Pinus uncinata* is intermingled with *Pinus sylvestris* ssp. *engadinensis*.

5.3.6 Prostrate pine scrub (*Pinus mugo* communities)

The main distribution area of *Pinus mugo* lies in the E-Alps. There, in the External Alps, the Intermediate Alps and on extreme sites of the Inner Alps it covers wide areas between 1800 and 2200 m a.s.l. (Wagner 1985). In avalanche paths and on boulder scree the species can reach down to the montane belt. In the W-Alps *Pinus mugo* occurs extremely rarely (Barbero et al. 1970; Ozenda 1988).

High floristic similarities to the *Pinus uncinata* communities can be observed (Mayer 1974; Wallnöfer 1993c). From shadowy, steep slopes on limestone or dolomite a Rhodothamno-Rhododendretum hirsuti was described with *Pinus mugo, Rhodothamnus chamaecistus, Rhododendron hirsutum, Sorbus chamaemespilus* and *Dryas octopetala*. The Erico carneae-Pinetum prostratae characterizes south-exposed scree areas. In this community species of the alpine grasslands are already present in the understorey together with the dwarf shrubs *Daphne striata* and *Juniperus communis* ssp. *alpina*.

On silicate stands mainly of the Inner and Intermediate Alps species-poor *Pinus mugo* communities appear on shallow rocky sites or on bolder scree. Here, *Rhododendron ferrugineum, Vaccinium* spp. and *Juniperus communis* ssp. *alpina* are the typical companion species.

5.3.7 Sycamore-beech forest (*Acer pseudoplatanus-Fagus sylvatica* communities)

Upper montane and subalpine sycamore-beech forests occur mainly in oceanic mountain chains characterised by high precipitation, thus in the northern and southern External Alps with main distribution in the NW-Alps (Kuoch 1954; Ott et al. 1997) and in Swiss Jura (Moor 1952). The community was described as Aceri-Fagetum and Saxifrago rotundifoliae-Fagetum (Willner 2002). Typical sites are steep slopes, furrows and boulder scree. Apart from *Acer pseudoplatanus* and *Fagus sylvatica,* also *Ulmus glabra, Picea abies* and rarely also *Abies alba* occur in the tree layer. According to the high air humidity of these stands the stems are covered abundantly by lichens (Reisigl and Keller 1989). On steep slopes snow pressure provokes a pronounced sabre (bow) form of the stems. Contorted and stunted growth can also be observed on sites near the timberline (Fanta 1981). *Sorbus aucuparia, Lonicera alpigena, L. nigra, Ribes alpinum, Rosa pendulina* are found in the shrub layer. In the S-Alps, for instance on the Monte Baldo, *Laburnum alpinum* and *L. anagyroides* are characteristic shrub species. Tall forbs dominate in the species-rich understorey.

5.3.8 Green alder and willow scrub

Due to the higher precipitations in the External and Intermediate Alps *Alnus alnobetula* (syn. *A. viridis*) is able to colonize moist stands in steep avalanche paths, along running water and small brooks at the timberline ecotone. In steep furrows *Alnus alnobetula* descends to the montane belt. The community Alnetum viridis is generally located on deep, moist and nutrient-rich soils (Oberdorfer 1978; Karner and Mucina 1993). These conditions are favourable for an abundant tall forb occurrence.

Along the streams tall willow communities may be developed nearly up to the timberline ecotone (*Salix pentandra, S. myrsinifolia, S. appendiculata*). Willow scrubs with low height extend from the timberline ecotone up to the lower alpine belt especially on north-exposed bolder scree slopes (*Salix waldsteiniana, S. caesia, S. foetida)* or on moraines (*Salix glaucosericea, S. helvetica, S. hastata, S. breviserrata*, Grabherr and Mucina 1993).

5.3.9 Dwarf shrub heath

On siliceous soils dwarf shrub heaths form a close mosaic with the remnant forest at the timberline ecotone (Schweingruber 1972). They belong to the class Loiseleurio-Vaccinietea (Grabherr 1993a). The small scale distribution of the dwarf shrub species depends on snow cover during winter and wind exposure, respectively. *Rhododendron ferrugineum* occupies the depression sites, *Vaccinium myrtillus, V. vitis-idaea, Arctostaphylos uva-ursi, Juniperus communis* ssp. *alpina* grow on more exposed slopes, *Vaccinium gaultherioides*, *Empetrum hermaphroditum* towards the wind-swept sites and on the extremely exposed stands a lichen heath with *Loiseleuria procumbens* (Creeping Azalea wind heath or chamois heath carpet, Ellenberg 1988) predominates.

5.3.10 Substitutional communities due to human landuse at the timberline

For hundreds of years the timberline ecotone has been influenced by human activities and regular landuse maintained more or less treeless zones. Extended species-rich substitutional communities can be found, i.e. dwarf shrub heaths with 30-40 vascular plant species or subalpine meadows and pastures showing up to 60 species (Ozenda and Borel 2003). Communities of the class Loiseleurio-Vaccinietea are among the most obvious ones. As secondary invaders after abandonment of the traditional landuse since the 1950s, these communities expanded also onto the meadows and pastures in the timberline ecotone. Especially the *Rhododendron ferrugineum*-heath spreaded all over the siliceous Inner Alps and indicates areas which have been forest in former times (Lüdi 1921). Dry slopes with high amounts of sunshine are secondarily colonized by a Junipero-Arctostaphyletum with *Calluna vulgaris, Juniperus communis* ssp. *alpina, Vaccinium* spp. and *Arctostaphylos uva-ursi* (Braun-Blanquet et al. 1954; Grabherr 1993a).

The main grassland communities in the potential forest area are those dominated by *Nardus stricta* (for instance the Sieversio-Nardetum strictae; Peppler-Lisbach and Petersen 2001). In the *Nardus stricta* grasslands elements from different communities co-dominate (i.e. species typical for Vaccinio-Piceetea, Mulgedio-Aconitetea, Molinio-Arrhenatheretea, Caricion curvulae). Vegetation mosaics of grassland patches, dwarf shrub heaths and forest patches or single trees are characteristic for most timberline sites in the Alps. Species of the alpine belt may be already present. Numerous grassland communities (mainly dominated by *Festuca* spp.) have been described from the transition zone between timberline and alpine belt (Grabherr 1993b). One of the most frequently occurring farmed grassland types in the timberline ecotone is the Crepido-Festucetum commutatae (Ellmauer and Mucina 1993). It can be found as herb-rich pasture or extensively mown hay meadow and is characterized by a mixture of lowland, montane and alpine grassland species.

References

Barbero G, Bono G, Ozenda P (1970) Confronto tra la vegetazione del versante settentrionale e quello meridionale delle Alpi Marittime e Liguri in rapporto ai fattori ecologici. Mitteilungen der Ostalpin-Dinarischen Gesellschaft für Vegetationskunde 11: 13-18

Bätzing W (2003) Die Alpen. Geschichte und Zukunft einer europäischen Kulturlandschaft. Verlag C.H. Beck, München

Béguin C, Theurillat J-P (1982) La forêt thermophile d'arolles. Candollea 37: 349-379

Bortenschlager S (1993) Das höchst gelegene Moor der Ostalpen ‚Moor am Rofenberg' 2760 m. Dissertationes Botanicae 196: 329-334

Brändli U-B (2000) Waldzunahme in der Schweiz – gestern und morgen. Informationsblatt Forschungsbereich Landschaft, Eidgenössiche Forschungsansalt WSL, Birmensdorf 45: 1-4

Braun-Blanquet J, Pallmann H, Bach R (1954) Pflanzensoziologische und bodenkundliche Untersuchungen im schweizerischen Nationalpark und seinen Nachbargebieten. II. Vegetation und Böden der Wald- und Zwergstrauchgesellschaften (Vaccinio-Piceetalia). Ergebnisse der wissenschaftlichen Untersuchungen des Schweizer Nationalparks, Nationalpark-Forschung 4

Breitenmoser U (1998) Large predators in the Alps: the fall and rise of man's competitor. Biological Conservation 83: 279-289

Del Favero R, Poldini L, Bortoli PL, Lasen C, Dreossi G, Vanone G (1998) La vegetazione forestale e la selvicoltura nella regione Friuli-Venezia Giulia, 2nd vol. Regione Autonoma Friuli-Venezia Giulia, Udine

Ellenberg H (1988) Vegetation ecology of central Europe, 4th edn. Cambridge University Press, Cambridge, New York, New Rochelle, Melbourne, Sydney

Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. Verlag Eugen Ulmer, Stuttgart

Ellenberg H, Klötzli F (1972) Waldgesellschaften und Waldstandorte der Schweiz. Mittteilungen der Schweizerischen Anstalt für das Forstliche Versuchswesen Zürich 48: 589-930

Ellmauer T, Mucina L (1993) Molinio-Arrhenatheretea. In: Mucina L, Grabherr G, Ellmauer T (eds) Die Pflanzengesellschaften Österreichs. Teil I. Anthropogene Vegetation. Fischer, Jena, Stuttgart, New York, pp 297-401

Ewald J (1999) Soziologie und Standortsbindung subalpiner Fichtenwälder in den Bayerischen Alpen. Tuexenia 19: 107-125

Fanta J (1981) *Fagus silvatica* L. und das Aceri-Fagetum an der alpinen Waldgrenze in mitteleuropäischen Gebirgen. Vegetatio 44: 13-24

Frehner M, Wasser B, Schwitter R (2005) Nachhaltigkeit und Erfolgskontrolle im Schutzwald. Wegleitung für Pflegemassnahmen in Wälder mit Schutzfunktion, Vollzug Umwelt. Bundesamt für Umwelt, Wald und Landschaft, Bern

Friedel H (1967) Verlauf der alpinen Waldgrenze im Rahmen anliegender Gebirgsgelände. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 75: 81-172

Frey H-U (1995) Waldgesellschaften und Waldstandorte im St. Galler Berggebiet. Veröffentlichungen Geobotanisches Institut ETH Stiftung Rübel, Zürich, 126 a+b

Grabherr G (1993a) Loiseleurio-Vaccinietea. In: Grabherr G, Mucina L (eds.) Die Pflanzengesellschaften Österreichs. Teil II. Natürliche waldfreie Vegetation. Fischer, Jena, Stuttgart, New York, pp 447-467

Grabherr G (1993b) Caricetea curvulae. In: Grabherr G, Mucina L (eds) Die Pflanzengesellschaften Österreichs. Teil II. Natürliche waldfreie Vegetation. Fischer, Jena, Stuttgart, New York, pp 343-372

Grabherr G, Mucina L (1993) Die Pflanzengesellschaften Österreichs. Teil II. Natürliche waldfreie Vegetation. Fischer, Jena, Stuttgart, New York

Hofmann A (1970) Die Höhengrenzen der Arve und der Arvenwälder in den Italienischen Alpen. Mitteilungen der Ostalpin-Dinarischen Gesellschaft für Vegetationskunde 11: 67-80.

Holtmeier F-K (2003) Mountain timberlines. Ecology, patchiness, and dynamics. Advances in Global Change Research, vol 14. Kluwer Academic Publishers, Dordrecht, Boston, London

Karner P, Mucina L (1993) Mulgedio-Aconitetea. In: Grabherr G, Mucina L (eds) Die Pflanzengesellschaften Österreichs. Teil II. Natürliche waldfreie Vegetation. Fischer, Jena, Stuttgart, New York, pp 468-505

Knapp R (1954) Über subalpine Buchenmischwälder in den nördlichen Ostalpen. Berichte der Bayerischen Botanischen Gesellschaft 30: 71-84

Kuoch R (1954) Wälder der Schweizer Alpen im Verbreitungsgebiet der Weißtanne. Mitteilungen der Schweizerischen Anstalt für das Forstliche Versuchswesen 30: 133-260

Kuoch R, Amiet R (1970) Die Verjüngung im Bereich der oberen Waldgrenze der Alpen. Mitteilungen der Schweizerischen Anstalt für das Forstliche Versuchswesen 46: 159-328

Kuoch R, Schweingruber FH (1975) Baumarten an der alpinen Waldgrenze in der Schweizerische Schweizer Zeitschrift für Forstwesen 126: 13-40.

Lüdi W (1921) Die Pflanzengesellschaften des Lauterbrunnentals und ihre Sukzession. Beiträge zur Geobotanischen Landesaufnahme der Schweiz 9

Mayer H (1962) Gesellschaftsanschluss der Lärche und Grundlagen ihrer natürlichen Verbreitung in den Ostalpen. Angewandte Pflanzensoziologie 17: 5-56

Mayer H (1974) Wälder des Ostalpenraumes. Gustav Fischer Verlag, Stuttgart

Mayer H (1986) Europäische Wälder. Fischer, Stuttgart, New York

Mayer H, Ott E (1991) Gebirgswaldbau Schutzwaldpflege. Fischer, Stuttgart, New York

Moor M (1952) Die Fagion-Gesellschaften im Schweizer Jura. Beiträge zur Geobotanischen Landesaufnahme der Schweiz 31: 1-201

Neuwinger I (1970) Böden der subalpinen und alpinen Stufe in den Tiroler Alpen. Mitteilungen der Ostalpin-Dinarischen Gesellschaft für Vegetationskunde 11: 135-150

Oberdorfer E (1978) Klasse: Betulo-Adenostyletea Br.-Bl. et Tx. 43. In: Oberdorfer E (ed) Süddeutsche Pflanzengesellschaften. Teil II, 2nd edn. Fischer, Stuttgart, New York, pp 329-341

Oberdorfer E (1992) Süddeutsche Pflanzengesellschaften. Teil IV: Wälder und Gebüsche. Textband, 2nd edn. Fischer, Jena, Stuttgart, New York

Odasso M (2002) I tipi forestali del Trentino. Centro di Ecologia Alpina, Sardagna

Ott E, Frehner M, Frey H-U, Lüscher P (1997) Gebirgsnadelwälder. Ein praxisorientierter Leitfaden für eine standortgerechte Waldbehandlung. Paul Haupt Verlag, Bern, Stuttgart, Wien

Ozenda P (1988) Die Vegetation der Alpen im europäischen Gebirgsraum. Fischer, Stuttgart, New York

Ozenda P, Borel J-L (1995) Possible responses of mountain vegetation to a global climatic change: the case of the Western Alps. In: Guisan A, Holten JI, Spichiger R, Tessier L (eds) Potential ecological impacts of climate change in the Alps and Fennoscandian Mountains. Publication hors-série n. 8 des Conservatoire et Jardin botaniques de la Ville de Genève, Genève, pp 137-144

Ozenda P, Borel J-L (2003) The alpine vegetation of the Alps. In: Nagy L, Grabherr G, Körner Ch, Thompson DBA (eds) Alpine biodiversity in Europe. Ecological Studies, vol 167. Springer, Berlin, Heidelberg, New York, pp 53-64

Patzelt G, Kofler W, Wahlmüller B (1997) Die Ötztalstudie – Entwicklung der Landnutzung. In: Alpine Vorzeit in Tirol. Begleitheft zur Ausstellung. Universität Innsbruck: 46-62

Pedrotti F, Gafta D (2003) The high mountain flora and vegetation of the Apennines and the Italian Alps. In: Nagy L, Grabherr G, Körner Ch, Thompson DBA (eds) Alpine biodiversity in Europe. Ecological Studies, vol 167. Springer, Berlin, Heidelberg, New, York, pp 73-84

Peppler-Lisbach C, Petersen J (2001) Synopsis der Pflanzengesellschaften Deutschlands Heft 8, Calluno-Ulicetea (G3) Teil 1: Nardetalia strictae, Borstgrasrasen. Verlag der Floristisch-soziologischen Arbeitsgemeinschaft e.V., Göttingen

Reisigl H, Keller R (1989) Lebensraum Bergwald. Fischer, Stuttgart, New York

Sakai A, Larcher W (1987) Frost survival of plants. Responses and adaptation to freezing stress. Ecological Studies, vol 62. Springer, Berlin, Heidelberg, New York

Schönenberger W (1981) Die Wuchsformen der Bäume an der alpinen Waldgrenze. Schweizer Zeitschrift für das Forstwesen 132: 149-162

Schütz M, Wildi O, Achermann G, Krüsi BO, Nievergelt B (2000) Predicting the development of subalpine grassland in the Swiss National Park: how to build a succession model based on data from long-term permanent plots. In: Schütz M, Krüsi BO, Edwards PJ (eds) Succession research in the Swiss National Park. Nationalpark-Forschung in der Schweiz 89, pp 207-235

Schweingruber FH (1972) Die subalpinen Zwergstrauchheiden im Einzugsgebiet der Aare (Schweizerische nordwestliche Randalpen). Mitteilungen der Schweizerischen Anstalt für das Forstliche Versuchswesen 48: 197-504

Wagner H (1985) Die Pflanzendecke Österreichs. Erläuterungen zur Vegetationskarte 1:1000000 im Österreich-Atlas. Österreichische Akademie der Wissenschaften

Walentowski H, Ewald J, Fischer A, Kölling C, Türk W. (2004) Handbuch der natürlichen Waldgesellschaften Bayerns. Verlag Geobotanica, Freising

Wallnöfer S (1993a) Vaccinio-Piceetea. In: Mucina L, Grabherr G, Wallnöfer S (eds) Die Pflanzengesellschaften Österreichs. Teil III. Wälder und Gebüsche. Fischer, Jena, Stuttgart, New York, pp 283-337

Wallnöfer S (1993b) Pulsatillo-Pinetea. In: Mucina L, Grabherr G, Wallnöfer S (eds) Die Pflanzengesellschaften Österreichs. Teil III. Wälder und Gebüsche. Fischer, Jena, Stuttgart, New York, pp 237-243

Wallnöfer S (1993c) Erico-Pinetea. In: Mucina L, Grabherr G, Wallnöfer S (eds) Die Pflanzengesellschaften Österreichs. Teil III. Wälder und Gebüsche. Fischer, Jena, Stuttgart, New York, pp 244-282

Willner W (2002) Syntaxonomische Revision der südmitteleuropäischen Buchenwälder. Phytocoenologia 32: 337-453

Zukrigl K (1973) Montane und subalpine Waldgesellschaften am Alpenostrand. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 101: 1-387

6 Limitation by an Insufficient Carbon Assimilation and Allocation

Gerhard Wieser

Institut für Naturgefahren und Waldgrenzregionen, BFW, Innsbruck

6.1 Introduction

Carbon compounds are the currency that plants accumulate, store, and use to build their structure and maintain their physiological processes (Waring and Schlesinger 1985). Trees differ from other plants with respect to carbon investments in productive tissues and support structures. Most of the biomass of a tree is accumulated in woody tissues that do not photosynthesize but support the foliage and the fine roots (Friend et al. 1994; Gower et al. 1995).

Costs for maintaining these supporting and conducting tissues are high in trees when compared to dwarf shrubs and herbaceous plants with their more favourable leaf mass ratio, i.e. the dry matter of leaves in % of total plant mass (Boysen-Jensen 1932; Ellenberg 1975; Stevens and Fox 1991; Slatyer and Noble 1992; Körner 1994, 2003a; Cairns 1998; Cairns and Malanson 1998).

Thus, beside carbon gain, carbon allocation might be of equal importance in determining the upper physiological limit of trees (Bernoulli and Körner 1999). As both processes interact (Waring and Schlesinger 1985), we briefly review the carbon cycle of a tree (Fig. 6.1).

Carbon begins to cycle when the tree assimilates atmospheric CO_2 through photosynthesis into reduced sugars. Canopy photosynthesis is determined by net photosynthetic activity and the total amount of the photosynthetic active leaf surface area or leaf mass of the foliage and is integrated over selected daily or seasonal time periods.

G. Wieser and M. Tausz (eds.), Trees at their Upper Limit, 79–129.

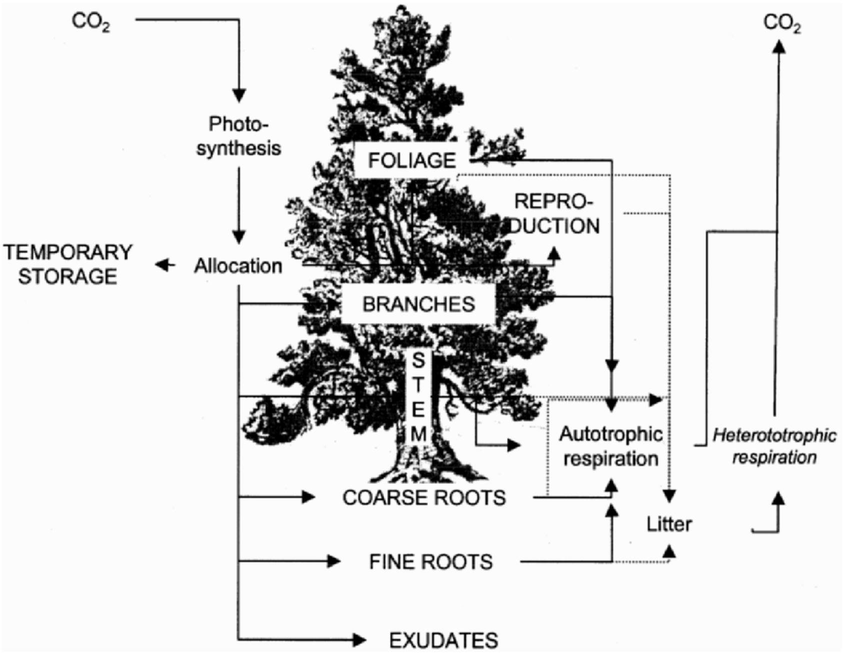

Fig. 6.1. Major components of the carbon balance of a tree including photosynthesis, autotrophic respiration (solid arrows), partitioning, and allocation into various components, losses of organic matter (dotted arrows), and associated heterotrophic respiration.

The maintenance of existing cells as well as the growth of new cells requires energy, and a large portion of the carbon fixed by photosynthesis is lost via autotrophic respiration.

Dry matter production, therefore, results from the balance between total canopy photosynthesis and the amount of carbon lost via autotrophic respiration. The remaining carbon can be allocated to various components and can be utilized for light capture (foliage), support (branches, stem, coarse roots), water and nutrient uptake (fine roots), reproduction (seeds and fruiting structure), and temporary storage of carbohydrates.

Losses of above ground organic matter due to dieback and shedding as well as fine-root turnover are the main contributors to litter, finally leading to an accumulation of soil humus, representing an important long term carbon storage pool in cold temperate forest ecosystems. Soil organic matter however, also supports microbes and animals, which through their heterotrophic metabolism release CO_2 back to the atmosphere.

6.2 Uptake and loss of carbon dioxide

Photosynthesis is the process by which plants absorb light energy and convert atmospheric CO_2 to carbohydrates that are available for further biochemical processes. In parallel, during daylight hours leaves also release CO_2 – through mitochondrial respiration as well as photorespiration, the latter linked to the oxygenase activity of the enzyme ribulose-bisphosphate carboxylase-oxygease (Rubisco) – so that there is a net CO_2 uptake, termed as apparent net photosynthesis. Net photosynthesis is regulated simultaneously by many factors.

Environmental factors, consisting primarily of light, temperature, humidity, CO_2, and other gases along with nutrients and sink demands have direct and indirect effects on net photosynthesis (Teskey et al. 1995). Finally, net photosynthesis is also dependent on plant internal factors, which determine the *net photosynthetic capacity* (A_{max}) i.e., the maximum rate of net photosynthesis that can be achieved *in situ* during a growing season under ambient CO_2 concentration and optimum conditions of temperature, irradiance, vapour pressure deficit, and soil water availability (Larcher 2001).

A large portion of the carbon fixed by net photosynthesis is lost by mitochondrial respiration for growth and maintenance. Growth respiration is defined as the carbon costs for constructing a particular type of tissue and the costs (g carbon respired per g carbon of new tissue) can be calculated by knowing the chemical composition according to the concept of Penning de Fries (1975). Maintenance or “dark respiration”, is the basal cost for maintaining established tissue (g carbon respired per g tissue within a certain time span) and is highly sensitive to temperature and also to the specific activity of organ types such as foliage, stems, branches, and roots.

6.2.1 Net photosynthetic capacity and specific respiratory capacity of trees in the timberline ecotone

Net photosynthetic capacity

Net photosynthetic capacity is a characteristic of plant species, ecotypes, and even individual varieties (Woodward and Smith 1994). Conifers generally have a lower net photosynthetic capacity than broadleaf trees. However, even among evergreen trees there are large variations, both within and between species. Table 6.1 contains net photosynthetic capacity rates of current year foliage of mature trees measured *in situ* in the timberline ecotone of central European Alps, New Zealand, and Australia. Rates range between 3 and 9 µmol m^{-2} s^{-1} and reflect differences in habitat conditions and leaf morphology.

Expressed per total needle area conifers have a lower net photosynthetic capacity than broadleaved trees (Table 6.1). But when values are converted to projected leaf area, which is approximately 2.6 times smaller than the overall total surface area of the needles, rates are comparable with values published for other values published for broadleaved trees in boreal, temperate, Mediterranean, and even tropical climates (Körner 1994; Larcher 2001).

Table 6.1. Net photosynthetic capacity (A_{max}) of current-year foliage measured *in situ* in the timberline ecotone of Europe (Klimahaus, Mt. Patscherkofel, 1950 m; Stillberg, Switzerland, 2185 m), New Zealand (Craigieburn Range, 1330 m) and Australia (Snowy Mountains, 1645 m). Data are related to total and projected leaf surface area in conifers and deciduous trees, respectively.

Species	Location	A_{max} [µmol m^{-2} s^{-1}]	Reference
Picea abies	Europe	2.9 - 4.1	Havranek and Wieser 1993; Koike et al. 1994; Wieser and Havranek 1996
Pinus cembra	Europe	2.6 - 4.9	Koike et al. 1994; Wieser 2004a; Wieser and Havranek 2001
Larix decidua	Europe	3.2 – 7.5	Benecke et al. 1981; Volgger 1975
Pinus mugo	New Zealand	3.48	Benecke and Havranek 1980
Pinus sylvestris	New Zealand	4.43	Benecke and Havranek 1980
Pinus contorta	New Zealand	4.43	Benecke and Havranek 1980
Larix decidua	New Zealand	4.43	Benecke and Havranek 1980; Benecke et al. 1981
Eucalyptus pauciflora	Australia	8.86	Slatyer and Morrow 1977

Beside species related differences, net photosynthetic capacity is also dependent on tree age (Yoder et al. 1994), leaf age (Reich et al. 1995), position within the canopy (Dang et al. 1997), and leaf morphology (Oren et al. 1986).

In the timberline ecotone on Mt. Patscherkofel near Innsbruck, 66 to 76-year-old trees displayed a 6 to 20 % lower *in situ* net photosynthetic capacity when compared to cospecific seedlings as shown for *Larix decidua*, *Pinus cembra* (Tranqullini and Schütz 1970), and *Picea abies* (Wieser unpublished). In evergreen conifers, net photosynthetic capacity also decreases with increasing needle age as shown for *Picea abies* and *Pinus cembra* trees from 2185 m a.s.l. in the Swiss Alps (Fig. 6.2; Koike et al. 1994).

Different microclimatic conditions within a tree's crown also influence leaf morphology, and there is a good correlation between net photosynthetic capacity and specific leaf mass (Oren et al. 1986) or specific leaf area (leaf area per g dry weight), respectively. For example, at the alpine timberline more sun-exposed current- and one-year-old needles (as reflected in a lower specific leaf area) of *Picea abies* are known to posses a higher net photosynthetic capacity than more shade-type needles (as reflected in a higher specific leaf area), even after exposure to the same light level (Fig. 6.3).

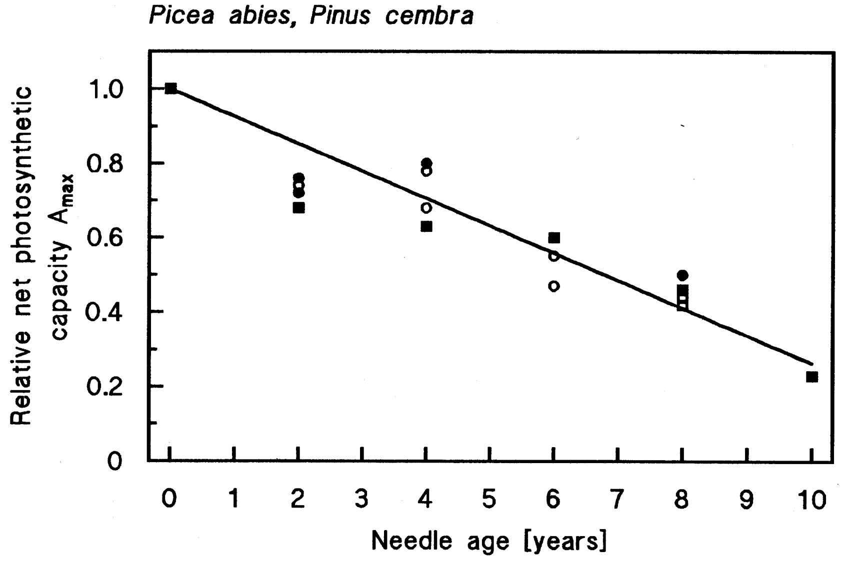

Fig. 6.2. Relative *in situ* net photosynthetic capacity in Norway spruce (*Picea abies*,●) and cembran pine (*Pinus cembra*,■) needles on a north-facing (closed symbols) and an east-facing slope (open symbols) in relation to needle age. Measurements were made at Stillberg, Switzerland, 2185 m a.s.l. Points were fit by linear regression: $y = 1 - 0.076 * x$, $r^2 = 0.90$. (Redrawn after Koike et al. 1994.)

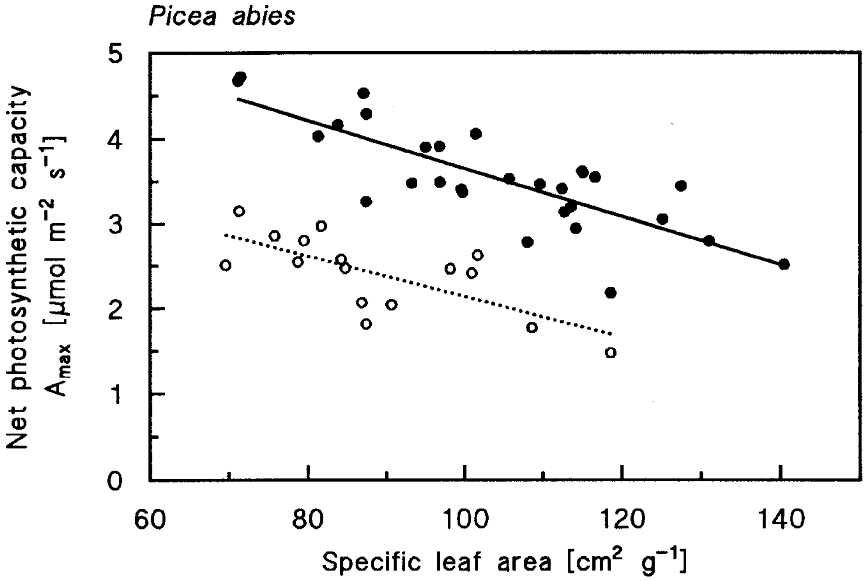

Fig. 6.3. Total needle area based *in situ* net photosynthetic capacity of current- (●) and one-year-old (○) Norway spruce (*Picea abies*) needles in relation to specific leaf area. Measurements were conducted at Mt. Patscherkofel (Klimahaus), Austria, 1950 m a.s.l. Points were fit by linear regression: current-year needles: y = -0.024 * x + 4.52, $r^2 = 0.5$; one year-old needles: y = –0.028 * x + 3.70, $r^2 = 0.65$. (Wieser unpublished 1988.)

There is an analogous situation in trees growing in relatively dense stands below the *forest line* (i.e. the upper limit of a continuous forest canopy). In temperate (Matyssek 1985), boreal (Dang et al. 1977), montane (Hollinger 1989), and Mediterranean (Gonzales-Rodriguez et al. 2001) forest ecosystems net photosynthetic capacity is greatest in the upper part of the crown and declines in parallel with irradiance towards the lower crown.

Conversely, as a function of light interception, specific leaf area increases from the top towards the bottom of the canopy (Morales et al. 1996; Hollinger 1989; Niinemets et al. 1999). On the other hand, in an open stand at the alpine timberline on Mt. Patscherkofel, Innsbruck, net photosynthetic capacity of current-year *Pinus cembra* needles did not differ significantly with respect to position within the canopy and approached 4.5 and 4.6 μmol m^{-2} s^{-1} in the upper sun and the lower shade crown, respectively (Wieser 2004a). In an open high elevation *Pinus canariensis* stand in Tenerife, Canary Islands, Peters (2001) also failed to find significant differences in net photosynthetic capacity between the upper and the lower canopy.

Specific activity of mitochondrial respiration

Foliar respiration There is an obvious but critical debate as to when foliar dark respiration should be measured: at night or during the day. Ryan (unpublished in Sprugel et al. 1995) found that respiration of 1-year old conifer foliage at a given temperature was 20 – 40 % lower at night than during the day after 1 hour of darkening. Among the many studies on respiration only few data have been measured *in situ* during the night. Night-time dark respiration rates of mature current-year conifer needles, which presumably reflect maintenance respiration only, distilled from seasonal courses of foliar gas exchange at the upper timberline in Austria and New Zealand are compiled in Table 6.2. Rates range between 0.38 and 1.07 µmol m^{-2} s^{-1} at a temperature of 15 ± 1 °C.

Table 6.2. Dark respiration (R_d) rates of current-year mature conifer needles related to total surface area measured in situ at 15 ± 1 °C at the upper timberline in Austria (Klimahaus, Mt. Patscherkofel, 1950 m) and in New Zealand (Craigieburn Range, 1330 m).

Species	Location	R_d [µmol m^{-2} s^{-1}]	Reference
Picea abies	Austria	0.48	Wieser unpubl.
Pinus cembra	Austria	0.38	Wieser 2004a.
Larix deciduas	Austria	0. 63	Wieser unpubl.
Pinus mugo	New Zealand	0.95	Benecke and Havranek 1980
Pinus sylvestris	New Zealand	1.07	Benecke and Havranek 1980
Pinus contorta	New Zealand	0.96	Benecke and Havranek 1980
Larix decidua	New Zealand	0.66	Benecke and Havranek 1980

Woody-tissue respiration *In situ* measurements of woody tissue respiration (stem, branches, and coarse roots) of trees in the timberline ecotone have been conducted in *Alnus viridis*, *Larix decidua*, *Picea abies*, *Pinus sylvestris*, *Pinus cembra, Sorbus aucuparia* (Mt. Patscherkofel, Austria; Schütz 1968; Havranek 1981, 1985; Wieser and Bahn 2004), and *Betula ermanii* (Mt. Fuji, Japan; Gansert et al. 2002).

All these studies indicate that total (maintenance and construction) woody-tissue respiration varies seasonally between trees and even between locations within an entire tree. Unfortunately, all these data are given per unit surface area or per unit dry weight. When expressed per unit surface area the respiratory activity at a given temperature in stems, branches, and coarse roots of different thickness increases with diameter; and when expresses on dry weight respiratory activity decreases as shown for *Pinus cembra* and *Larix decidua* by Tranquillini and Schütz (1970) because the number of living cells in the xylem and phloem increases with decreasing diameter. Thus, the easiest way for comparing specific woody tissue respiration activities would be values of maintenance respiration per sapwood volume measured during the dormant season when growth has ceased, and construction respiration estimated per unit of newly produced woody tissue (cf. also Sprugel et al. 1995).

Unfortunately, for the timberline ecotone such data of maintenance respiration are presently only available for *Pinus cembra* (Wieser and Bahn 2004). These data suggest, that sapwood volume based maintenance respiration is relatively constant within the stem and coarse roots at diameters > 80 mm, while in thinner branches and twigs within the crown rates were up to 70-fold higher than at the stem base (Fig. 6.4). The higher respiration rates of branches and twigs in the outer sections of the crown might be due to a decrease in wind velocity and hence also an increase in the boundary layer conductance (Martin et al. 1999) with increasing depth of the canopy, both horizontal and vertical.

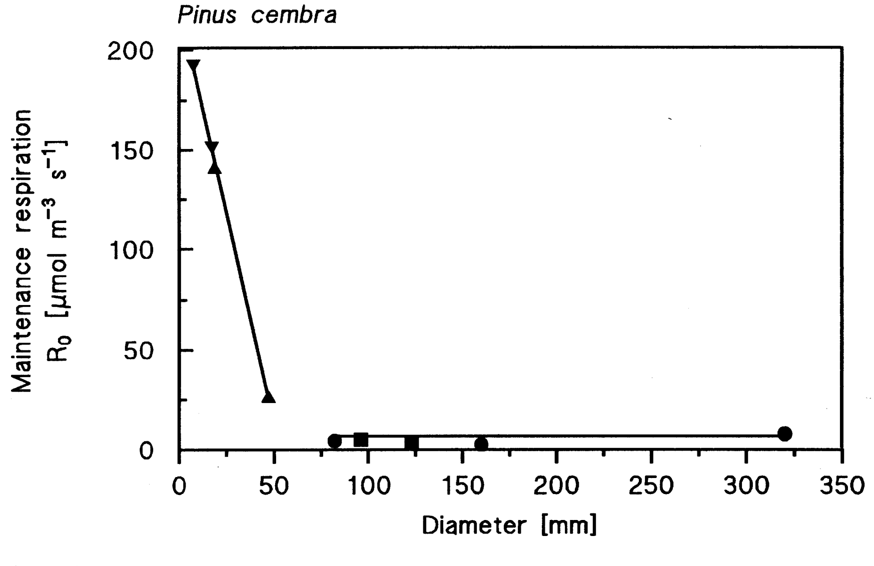

Fig. 6.4. Maintenance respiration per sapwood volume at a tissue temperature of 0 °C of coarse roots (■), stem sections (●), branches (▲), and twigs (▼) in an entire *Pinus cembra* tree as a function of diameter. Measurements were recorded during the dormant season (December – February) at Mt. Patscherkofel (Klimahaus), Austria, 1950 m a.s.l. (Modified after Wieser and Bahn 2004.)

Construction respiration costs of wood production at the alpine timberline on Mt. Patscherkofel are 1.19 g C per g C in *Pinus cembra* (Wieser et al. 2005) and 0.9 - 1.68 g C per g C in *Larix decidua* (Havranek 1985). The observation that these two construction respiration rates are significantly above the value based on the chemical pathway analysis (≈0.25 g C per g C; Penning de Vries 1775) suggest that beside direct chemical costs (carbohydrate phloem loading and unloading) additional respiratory costs might be involved in tissue production. Thus, more studies are needed in order to examine the actual costs of wood production at the timberline.

Fine root respiration Because of the inaccessibility of roots under natural conditions respiration of fine roots (ranging in diameter from < 1 to 6 mm; Sprugel et al. 1995) is much more difficult to measure than foliage or woody-tissue respiration.

Nearly all measurements have been made under laboratory conditions with excised roots collected from seedlings grown in pots or from the soil of a natural stand within the timberline ecotone of the central European Alps (Tranquillini 1959a, b; Keller 1967; Eccher 1972; Harrasser 1976; Framba 1980). Published rates of conifer fine root respiration measured at 15 °C along with the corresponding diameter sizes are summarised in Table 6.3.

Table 6.3. Fine and small-diameter root respiration rates at 15 °C for timberline associated conifer seedlings. Measurements were made under laboratory conditions using excised roots.

Species	Size class [mm]	R [mg g d_w^{-1} h^{-1}]	Reference
Picea abies	0 – 1	0.64	Harrasser 1976
	1 – 2	0.19	
	2 – 5	0.08	
	> 5	0.184	
	Fine	0.81	Keller 1967
	Fine	0.61	Framba 1980
Pinus cembra	0 – 1	0.43	Harrasser 1976
	1 – 2	0.09	
	2 – 5	0.05	
	> 5	0.10	
	Fine	0.55	Keller 1967
Larix decidua	0 – 1	0.57	Harrasser 1976
	1 – 2	0.20	
	2 – 5	0.09	
	> 5	0.09	
	Fine	0.29	Keller 1967
Pinus mugo	Fine	0.43	Keller 1967

In *Pinus cembra*, *Picea abies*, and *Larix decidua*, roots < 1 mm in diameter have a considerably higher respiration rate as compared to larger roots (see Table 6.3), the latter also displaying a higher degree of lignification (Harrasser 1976).

Plant development also affects root respiratory activity and as trees become older carbon allocation patterns will change, and this will be reflected in the respiratory demand of tissues. Framba (1980) found that in both *Picea abies* and *Pinus cembra* root respiration rates of 4-year old seedlings was higher than in 22-year old trees. Respiration rates also change in response to an altered environment, as does photosynthesis and sink metabolism. In *Picea abies* and *Pinus cembra* seedlings root respiration was highest when shoots were illuminated, strongly suggesting that apparent root respiration activity is directly dependent on the supply of photosynthate from the foliage (Eccher 1972; Framba 1980).

6.2.2 Net photosynthetic capacity and specific respiratory activity with respect to altitude

A comparison of CO_2 uptake rates from trees in the timberline ecotone with that from lower elevation sites needs to take into account that total atmospheric pressure and hence also the partial pressure of CO_2 decreases almost linearly by approximately 11% per 1000 m of altitude. However, a decrease in the partial pressure of CO_2 does not occur in isolation and is accompanied by other altitudinal changes in climatic parameters. The partial pressure of water vapour decreases rather more rapidly with altitude because of condensation as air temperature falls (cf. Chap. 2). All these changes affect the driving forces for gas diffusion via the stomata. Although, temperature and pressure effects are in opposite directions, the pressure effect is dominant and hence the diffusion coefficient increase with altitude (cf. also Jones 1991).

When measured at their local CO_2 partial pressure conifers in the timberline ecotone of central Europe have an *in situ* net photosynthetic capacity similar to that of their relatives at lower elevation sites (Fig. 6.5). No differences in photosynthetic capacity were also obtained for *Larix decidua* trees along an elevational transect in the Craigieburn Range, New Zealand (Benecke et al. 1981).

Mooney et al. (1964) also failed to find significant differences between net photosynthetic capacity of conifers growing at 2580 (*Pinus monophylla*) and 3240 m a.s.l. (*Pinus aristata*, *Pinus flexilis*) in the White Mountains of California.

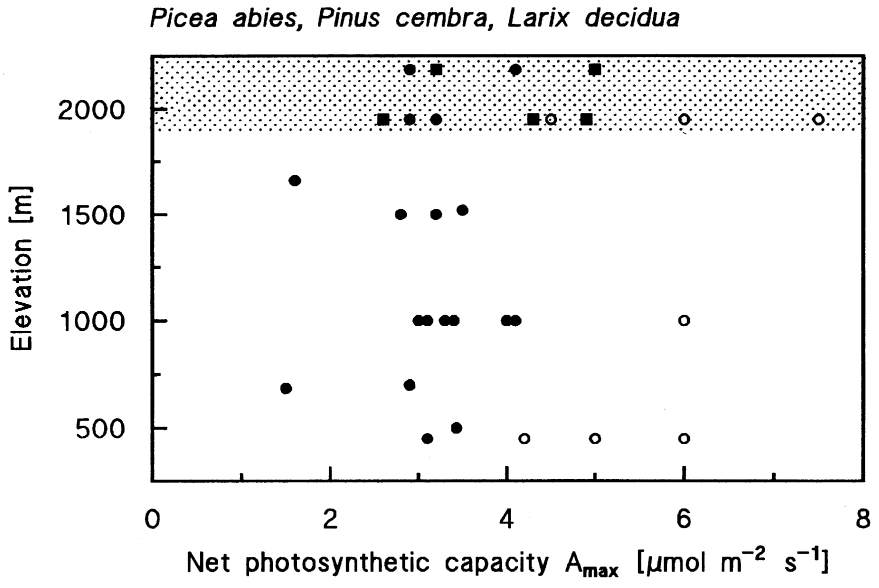

Fig. 6.5. *In situ* net photosynthetic capacity based on total surface area of current-year needles of adult Norway spruce (*Picea abies*, ●), cembran pine (*Pinus cembra*, ■), and European larch (*Larix decidua*, O) trees in the central European Alps between 450 and 1950 m a.s.l. (After data from Benecke et al. 1981; Matyssek 1985; Bolhar-Nordenkampf and Lechner 1889; Häsler et al. 1991; Havranek and Wieser 1993; Koike et al. 1994; Volgger 1995; Wieser and Havranek 1996, 2001; Wieser et al. 2002; and Wieser 2004a.)

When measured *in situ* under equal CO_2 partial pressure trees at the alpine timberline displayed significantly higher net CO_2 uptake rates as compared to trees at a low elevation site as shown for *Picea abies* in the central European Alps (Fig. 6.6) and for *Espeletia schutlztii* along an altitudinal gradient in the Venezuelan Andes (Rada et al 1998). This indicates a higher efficiency of carbon uptake per unit leaf area. Equal net photosynthetic capacity and higher carboxylation efficiency in trees at the upper timberline per unit leaf area might be due to altitude related differences in needle morphology. In the timberline ecotone conifers often produce less specific needle area per unit needle dry mass (Benecke et al. 1981; Hurtin and Marshall 2000; Richardson et al. 2001). For example, in *Picea abies* the specific leaf area of current-year needles decreased from 186 to 104 cm^2 total surface area per g dry weight between 1000 and 1950 m a.s.l. (Wieser unpublished 2002).

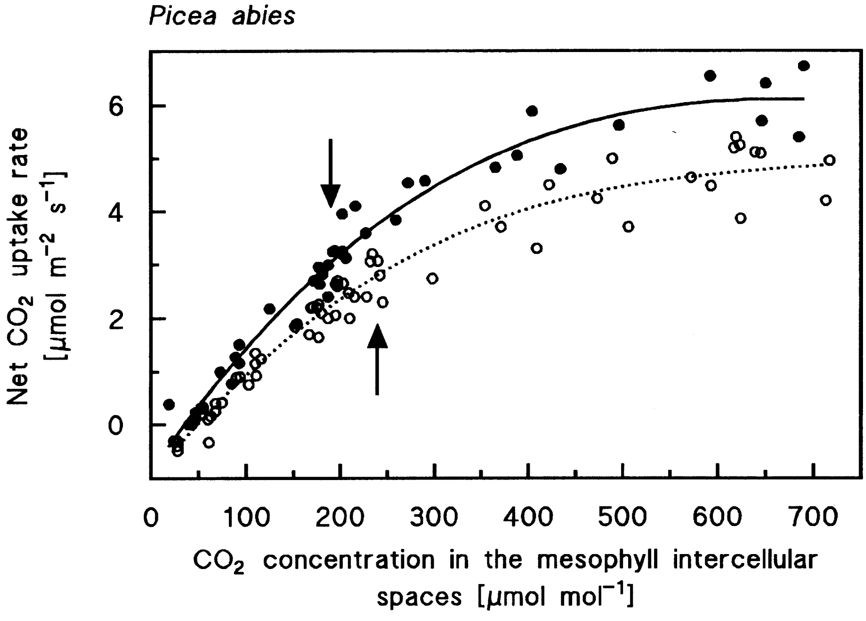

Fig. 6.6. The relationship between total needle area based net CO_2 uptake rate and the CO_2 concentration in the intercellular spaces of the mesophyll ("internal CO_2 partial pressure") of current-year shoots of Norway spruce (*Picea abies*) at 1950 (●) and 1000 (○) m a.s.l. Arrows indicate measurements at the local CO_2 partial pressure. (Wieser unpublished 1994.)

Needles of trees at high elevation sites also tend to have similar or higher nitrogen concentrations per unit dry mass when compared to lower elevation sites (Sparks and Ehleringer 1997; Richardson et al. 2001). The combination of a lower specific leaf area (≈ thicker needles) and a high foliar nitrogen concentration might cause the amount of photosynthetic enzymes per unit needle area to increase with altitude. Thus, trees at timberline have a greater demand for CO_2 which is also reflected in an increase of $\delta^{13}C$ as shown for *Pseudotsuga mesziesii*, *Abies lasiocarpa*, *Picea engelmanii* and *Pinus contorta* needles along an elevational gradient in the Rocky Mountains by Hurtine and Marshall (2000).

By *evolutionary temperature adaptation* net photosynthesis and respiration also adapt to the average temperature conditions of the environment of a tree (Larcher 2001). Leaves of trees at timberline in Europe (Pisek et al. 1969, 1973), Australia (Slatyer 1978), and New Zealand (Benecke and Havranek 1980) display a significantly lower ecotype-specific temperature optimum of net photosynthesis than leaves from trees at lower elevation sites. In general, the lapse rate of the temperature optimum for net photosynthesis parallels the adiabatic lapse rate in mean air temperature during the summer months as shown for the central European Alps in Fig. 6.7.

It is an old debate whether or not trees in the timberline ecotone respire more than trees in lowlands (Tanquillini 1979). At the same measurement temperature respiratory CO_2 losses of foliage (Pisek and Winkler 1958; Benecke and Havranek 1980; Mc Laughlin et al. 1991) and branches (Gansert et al. 2002) during the growing season are higher in trees at the timberline than at lower elevations (Fig. 6.8). However, when measured at the prevailing mean temperature trees experience in their local habitat respiration rates of trees at timberline are similar or even lower than at lower elevation sites (Fig. 6.8) as also observed by Larcher (1961) in evergreen trees growing in different climatic regions.

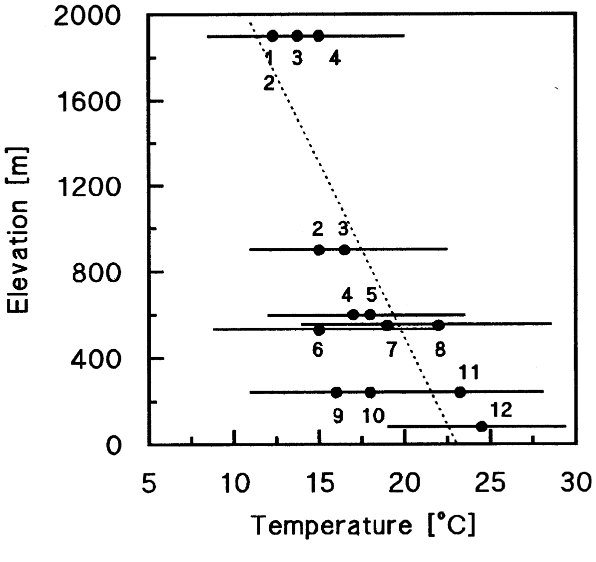

Fig. 6.7. Examples for the temperature optimum of net photosynthesis (●) and the temperature range where net photosynthesis is more than 90% of the maximum (horizontal bars) of different tree species with respect to elevation in the central European Alps. Species: (1) *Pinus cembra,* (2) *Picea abies,* (3) *Larix decidua,* (4) *Betula pendula,* (5) *Fagus sylvatica,* (6) *Abies alba,* (7) *Taxus baccata,* (8) *Laurocerasus officinalis,* (9) *Quercus ilex,* (10) *Olea europaea,* (11) *Quercus pubescens,* (12) *Citrus limonum.* The dotted line indicates the adiabatic lapse rate of the mean air temperature during the summer months (June, July, and August). (Redrawn after data from Pisek et al. 1969, 1973; and Fliri 1975.)

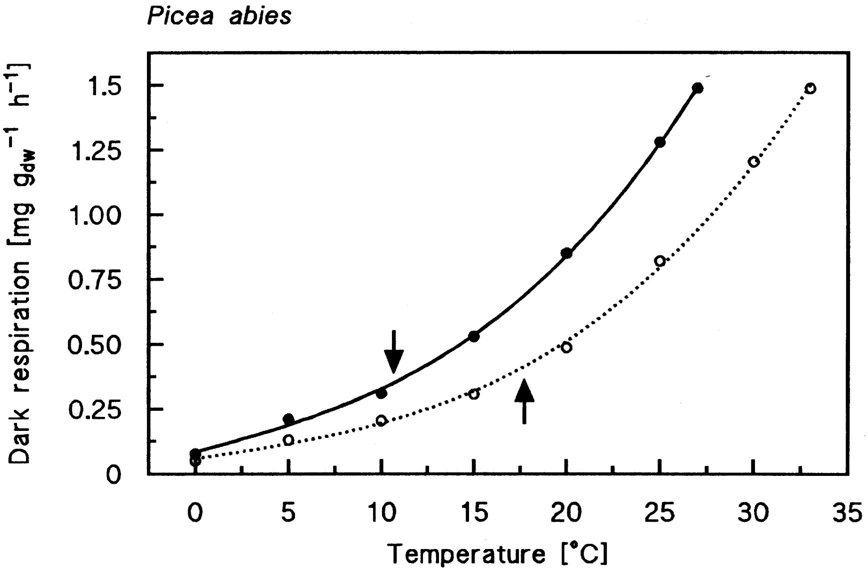

Fig. 6.8. The relationship between dark respiration and temperature of current-year shoots of Norway spruce (*Picea abies*) at 1840 (solid line and ●) and 1000 (dotted line and ○) m a.s.l. Measurements were made during the summer under laboratory conditions using excised twigs. Note the similar respiration rates at the locally prevailing temperature conditions, as indicated by arrows. (Modified after Pisek and Winkler 1958.)

Thermal acclimation to low temperatures allows timberline trees to achieve a similar energy supply at low temperatures which trees in valleys would reach only at significantly higher temperatures. Long-term thermal acclimation to lower temperature conditions at high elevations is also reflected in the specific activity of maintenance respiration.

For example, during the dormant season *Picea abies* needles at the timberline respire at similar rates per unit dry weight as in the valley and approach 0.03 and 0.04 mg CO_2 per g dry weight and hour, respectively (Pisek and Winkler 1958).

Similarly, branch maintenance respiration of *Betula ermanii* trees growing between 1600 and 2450 m a.s.l., i.e. the lower and upper distribution limit, varied by less than 0.1 µmol CO_2 m^{-2} s^{-1}, although the mean annual temperature decreases from 11.7 to 3.4 °C along this elevational gradient (Gansert et al. 2002).

6.2.3 Environmental constraints of carbon dioxide gas exchange

Net photosynthetic capacity and specific respiration activity generally refer to optimum life conditions. Seasonal and diurnal variations in CO_2 gas exchange however, are an overall expression of the interplay of a number of external factors. Variations in net photosynthesis are mainly dependent on irradiance, temperature, and humidity; and in general one of these factors is usually limiting CO_2 uptake at any given time throughout a year, while the others continue to exert a sub-threshold influence. Variations in respiration by contrast, are mainly driven by temperature.

Foliar gas exchange

Inter-annual variations in foliar gas exchange of trees at the alpine timberline have been investigated using cut twigs under laboratory conditions (Cartellieri 1935; Pisek and Winkler 1958) and *in situ* under field conditions (Benecke and Havranek 1980; Benecke et al. 1981; Havranek 1981; Tranquillini 1959a, b, 1962; 1964; Häsler 1994; Wieser 1997, 2004a). As an example, typical seasonal variations in environmental factors, daily maximum net photosynthesis, and night-time respiration of *Pinus cembra* needles of an adult tree growing at the alpine timberline (1950 m a.s.l.) on Mt. Patscherkofel near Innsbruck, Austria are shown in Fig. 6.9.

CO_2 gas exchange is highest during the growing season. In late autumn and early winter, gas exchange permanently declines in parallel with shorter days, lower irradiance, and near-freezing temperatures. The same factors also cause the development of frost resistance and cellular alterations during pre-dormancy (cf. Havranek and Tranquillini 1995 for a review). During the period of full winter dormancy gas exchange is almost completely suppressed. Recovery begins in spring in response to the diminishing occurrence of frost, higher air and stem temperatures, soil thawing as well as an adequate water utilisation (Tranquillini 1957; Havranek 1972; Wieser 1997). These findings are consistent with chlorophyll fluorescence measurements. The potential efficiency of photosystem II (F_V/F_m) in *Picea abies* and *Pinus cembra* has been shown to be significantly lower during the winter when compared to summer values (Stecher et al. 1999).

Low temperatures are the most important factors determining seasonal variations in foliar gas exchange in the timberline ecotone. At a given temperature net photosynthesis and night-time respiration are substantially lower during winter, spring, and autumn (Wieser 1997) than in summer (Pisek and Winkler 1958; Wieser 2004a). In the frost hardy stage the minimum temperature for CO_2 uptake ranges from -3 to -5 °C (Pisek et al.

1967) and net photosynthesis ceases completely upon freezing of the tissue water (Larcher 2001). Night-time respiration by contrast could be demonstrated down to -19 °C (Wieser 1997).

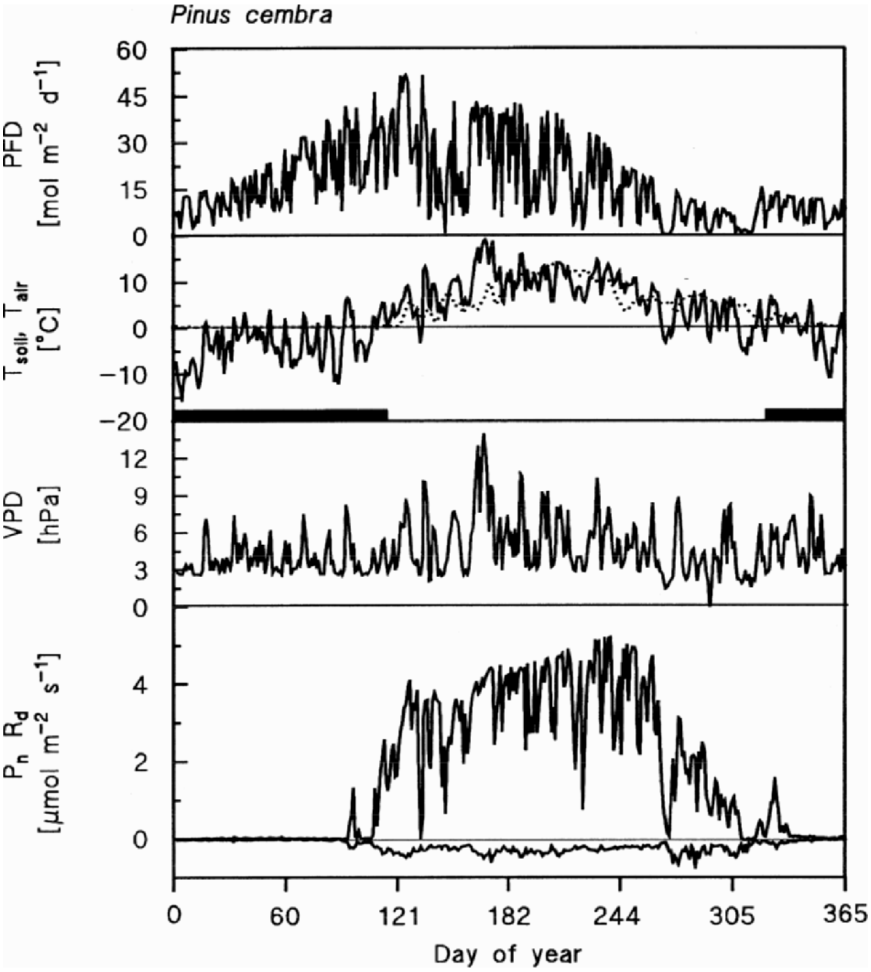

Fig. 6.9. Examples of inter-annual courses of daily sums of photon flux density (PFD), daily mean air- (T_{air}; solid line), and soil temperature (T_{soil}; dotted line), vapour pressure deficit (VPD), as well as daily maximum net photosynthesis (P_n), and night-time respiration (R_d) in current to two-year old needles of an adult *Pinus cembra* tree. The period of permanent snow cover is shown by horizontal bars. Measurements were conducted at Mt. Patscherkofel (Klimahaus), Austria, 1950 m a.s.l. (Modified after Wieser 1997 and 2004a.)

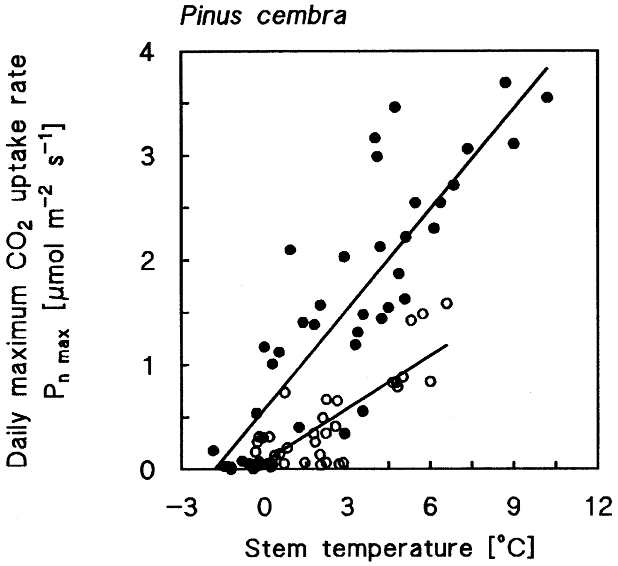

Fig. 6.10. The relationship between daily maximum net photosynthesis of current to two-year old needles of an adult *Pinus cembra* tree and the previous nigh minimum stem temperature 5 cm under the stem surface, 1.5 m above ground during spring (●) and autumn (O). Measurements were conducted at Mt. Patscherkofel (Klimahaus), Austria, 1950 m a.s.l. Points were fit by linear regression: spring: $y = 0.32 * x + 0.57$, $r^2 = 0.75$; autumn: $y = 0.17 * x + 0.06$, $r^2 = 0.70$. (Modified after Wieser 1997.)

Even short periods of apparently favourable climatic conditions during the cold season following a severe frost do not result in CO_2 uptake in the timberline ecotone (Pisek and Winkler 1958; Tranquillini 1957, 1979; Schulze et al. 1967; Traquillini and Machl-Ebner 1971; Schwarz 1971) as well as in the boreal zone (Ungerson and Scherdin 1968). Even when branches were transferred from the field to optimum laboratory conditions during the winter, net photosynthesis does not recover to full summer values (Pisek and Winkler 1958; Schwarz 1971). Thus, net photosynthesis during winter is not only suppressed by low temperatures but also by an endogenous factor that is not lost when branches are excised. These findings are consistent with chlorophyll fluorescence measurements (Nagele 1989).

Although a strict photosynthetic dormancy appears to be a characteristic of trees in the timberline ecotone (Tranquillini 1979) metabolic activity has been shown to increase during long lasting warm periods in late winter and net photosynthetic rates can reach up to 30 and 15 % of summer values in *Pinus cembra* and *Picea abies* needles, respectively when minimum air temperatures are above zero, and the soil, the stem, the branches, and the needles are not frozen (Wieser 1997).

During spring and autumn daily maximum net photosynthesis in adult *Pinus cembra* trees has been shown to be best correlated with the minimum stem temperature of the previous night until 10 °C was reached (Fig. 6.10; Wieser 1997). Over the same temperature range the spring increase in carbon dioxide uptake appeared to be more abrupt than the autumn decline (Fig. 6.10).

During spring recovery Havranek (1972) found a linear correlation between *in situ* sums of daily net photosynthesis of *Pinus cembra* seedlings and daily mean soil temperature at 10 cm soil depth between 0 and 7 °C (Fig. 6.11). Higher minimum night and mean root zone temperatures however, lose their role as a limiting factor for daily maximum net photosynthesis and carbon gain.

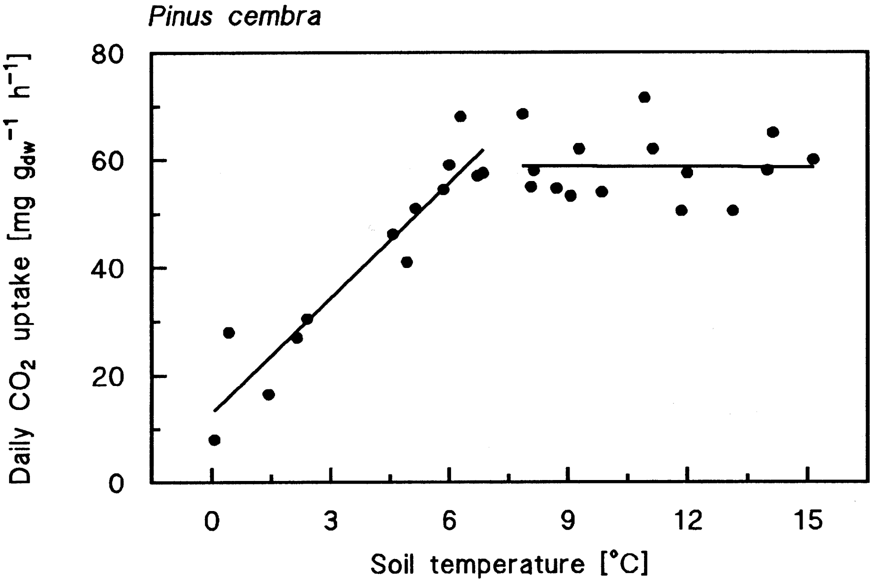

Fig. 6.11. The relationship between total daily CO_2 uptake of *Pinus cembra* seedlings and daily mean soil temperature at 10 cm depth. Measurements were conducted near the treeline at Obergurgl, Austria, 2070 m a.s.l. Points in the 0-7 °C temperature range were fit by linear regression: $y = 7.12 * x + 12.92$, $r^2 = 0.90$. (Modified after Havranek 1972.)

During the growing season however, when gas exchange is not hindered by low temperatures, lack of light is the major factor limiting net photosynthesis (Fig. 6.12). During all the daylight hours of an entire growing season photosynthetic photon flux density at the alpine timberline has been shown to be below light saturation (< 650 µmol m^{-2} s^{-1}) for approximately 40 % and supra-optimal for further 18 to 26 % (Turner 1961; Wieser 2004a). The latter is because in the field high irradiance is generally coupled with high temperatures and low atmospheric humidity. Under such conditions vapour pressure deficit indirectly limits CO_2 uptake, because a feed forward response to humidity causes leaf conductance to decline with increasing evaporative demand (Cowan 1977; Farquhar 1978). This reduction in stomatal conductance limits the diffusion of CO_2 into the leaves and hence net photosynthesis also declines with increasing vapour pressure deficit (Fig. 6.12).

Thermal limitation of CO_2 uptake during the growing season by contrast, is relatively unimportant because the temperature response curve of net photosynthesis is relatively wide (Fig. 6.12) and photosynthesis operates at more than 90% of its maximum over a range of 8 to 10 K (cf. Fig. 6.7). In reality, thermal limitation of net photosynthesis is primarily restricted to situations during which carbon uptake is restricted by low irradiance because the temperature optimum for carbon uptake shifts with irradiance towards lower values when photon flux density is low and towards higher values when photon flux density is high (Pisek and Winkler 1958; Pisek et al. 1969; Wieser 1977). Although trees are able to adapt to a wide range of seasonal temperature variations, extremes are more critical in limiting photosynthesis than mean temperatures. Night frosts significantly reduce net photosynthesis on the following day as shown for *Pinus cembra* by Tranquillini (1957) and the reduction in CO_2 uptake is directly related to the severity of the frost experienced by the trees (Pisek and Kemnitzer 1968; Bauer et al. 1969).

Soil moisture also affects net photosynthesis. Soil moisture deficits causing drought stress significantly decreased net photosynthesis of potted high altitude provenances of *Pinus cembra*, *Picea abies* and *Larix decidua* seedlings (Havranek and Benecke 1978; Wieser and Kronfuss 1997). This is because the primary physiological response to water limitation is stomatal closure, and thus diminishing CO_2 gas-exchange. In all the three species net photosynthesis began to decline at a soil water potential of -0. 4 MPa and CO_2 uptake approached zero at soil water potentials of -1.5 (*Pinus cembra*, *Picea abies*) to -1.9 (*Larix decidua*) MPa (Fig. 6.13) due to complete stomatal closure as well as to direct effects of water shortage (Kaiser 1987, Larcher 2001) and possible effects on electron transport and photophosphorylation.

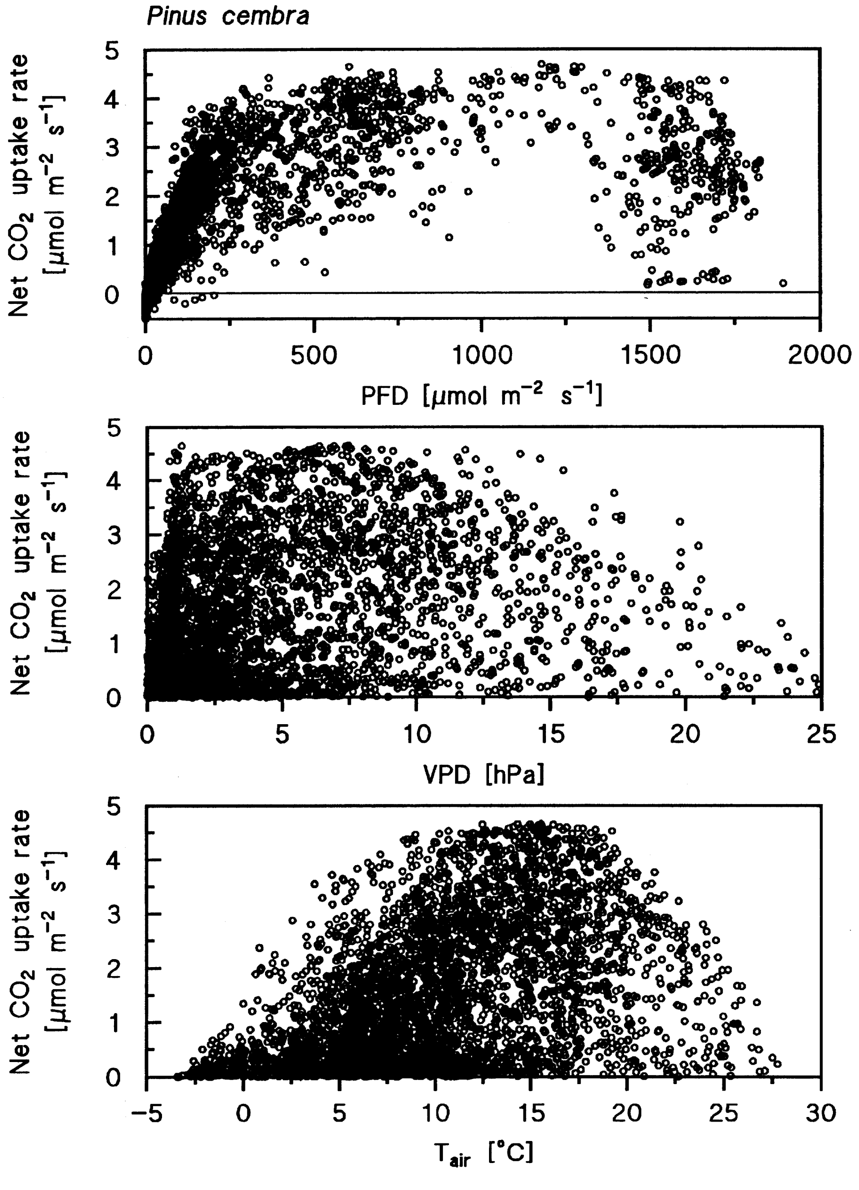

Fig. 6.12. The relationship between net CO_2 uptake rate of current to two-year old needles of an adult *Pinus cembra* tree and photon flux density (PFD), vapour pressure deficit (VPD), and air temperature (T_{air}), respectively. Measurements were conducted at Mt. Patscherkofel (Klimahaus), Austria, 1950 m a.s.l. (Modified after Wieser 2004a.)

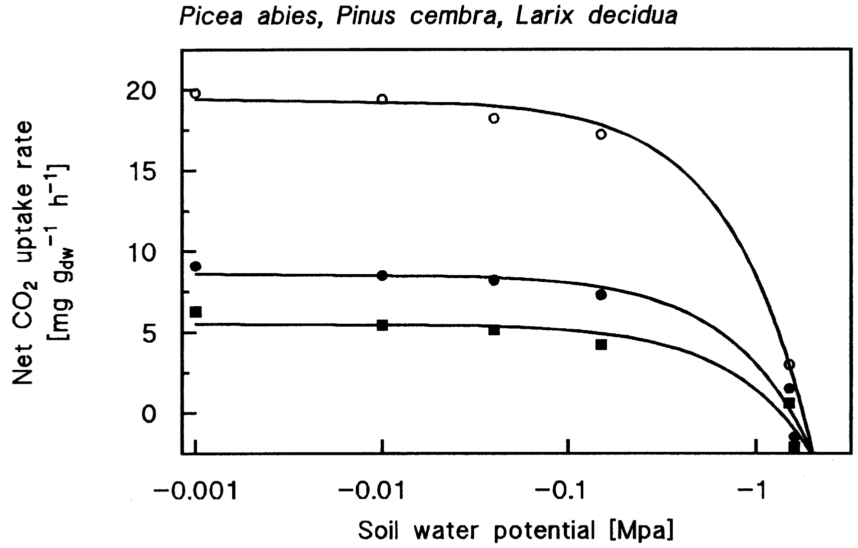

Fig. 6.13. Net photosynthesis of Norway spruce (*Picea abies*, ●), cembran pine (*Pinus cembra*, ■), and European larch (*Larix decidua*, ○) seedlings in relation to soil water potential. (Modified after Havranek and Benecke 1978.)

In the timberline ecotone however, soils rarely become dry enough for limiting net photosynthesis (Tranquillini 1979). In the timberline ecotone of the Central European Alps soil moisture seldom drops to values lower than 20 % volume, (i.e. soil water potential > -0.01) MPa (Gunsch 1972; Neuwinger 1970, 1980; Guggenberger 1980; Neuwinger-Raschendorfer 1961; Markart 2000; Wieser 2004b), even during the Central Europe-wide extremely dry summer of 2003.

Wind is also a particularly well-known environmental factor affecting net photosynthesis. Tranquillini (1969) subjected well watered *Picea abies*, *Pinus cembra* and *Larix decidua* seedlings in a phytotron to wind velocities ranging from 0.5 to 20 m s^{-1}. Initially, net photosynthesis increased by 4 (*Picea abies*) to 8 % (*Pinus cembra* and *Larix decidua*) at winds velocities between 1.5 and 10 m s^{-1}. At higher wind velocities however, net photosynthesis declined and approached 90 (*Picea abies*, *Larix decidua*) to 75 % (*Pinus cembra*) at a wind velocity of 20 m s^{-1} when compared to a wind velocity of 0.5 m s^{-1}. The observed initial increase in net photosynthesis can be attributed to wind induced changes in the atmosphere surrounding the needles, such as boundary layer, as well as gradients in leaf to air water vapour and CO_2 concentration (cf. also Telewski 1995).

All these factors have an effect on the diffusion of CO_2 from the atmosphere into the needle mesophyll. Conversely, the decline in net photosynthesis at wind velocities higher than 10 m s^{-1} can - beside partly stomatal closure (Tranquillini 1969; Caldwell 1970a) - mainly be attributed to a wind induced clustering of the needles, so that their display to available irradiance is impaired (Caldwell 1970b). Thus, net photosynthesis of freestanding tall trees might also frequently be limited during exposure to high wind velocities (Tranquillini 1969). On the other hand, wind also has an effect on convective heat loss and evaporative cooling. In addition, it is also well known that irradiance considerably raises stem and leaf temperatures, especially under low wind conditions (Tranquillini and Turner 1961; Hadley and Smith 1987; Gross 1989), and consequently also CO_2 uptake.

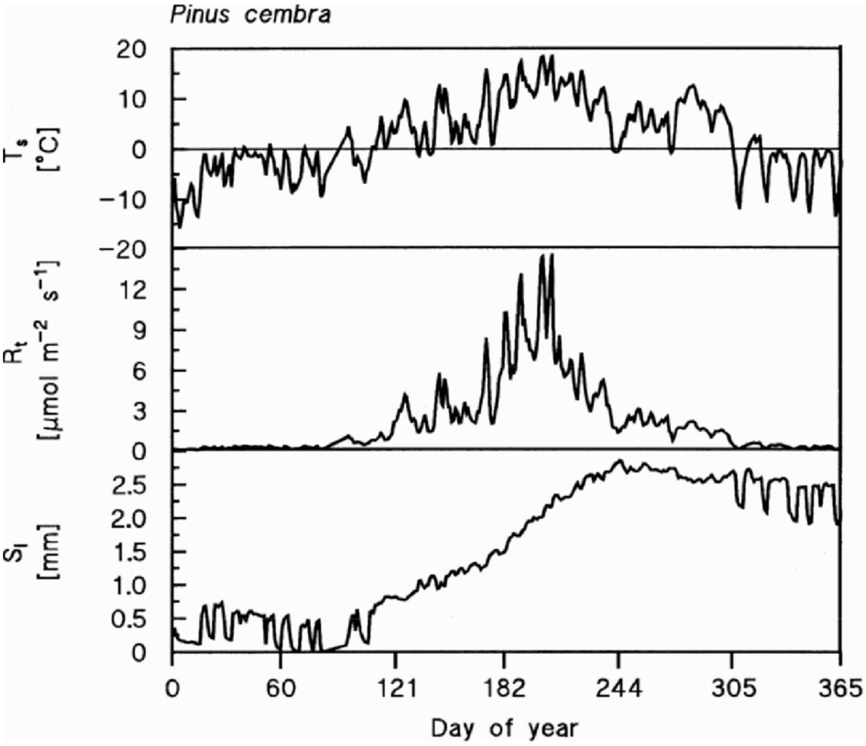

Fig. 6.14. Time course of sapwood temperature (T_s), daily mean total stem respiration (R_t), and radial stem growth increment (S_i) at breast height in an adult *Pinus cembra* tree. Measurements were made at Mt. Patscherkofel (Klimahaus), Austria, 1950 m a.s.l. (Modified after Wieser 2002.)

Woody-tissue and fine root respiration

Woody-tissue respiration also changes with the transition between active and dormant periods of a tree. Data available for *Larix decidua* (Havranek 1985) and *Pinus cembra* (Havranek 1981; Wieser 2002; Wieser and Bahn 2004) so far suggest that most of the annual variation in woody-tissue respiration reflects variations in growth and sapwood production at any given time.

In general, woody-tissue respiration is highest during the growing season and reduced to the level of maintenance respiration during the dormant period as shown for stem respiration of a *Pinus cembra* tree in Fig. 6.14. The seasonal pattern of stem respiration coincided with the pattern of radial increment growth (Fig. 6.14) as also observed in *Larix decidua* (Havranek 1985).

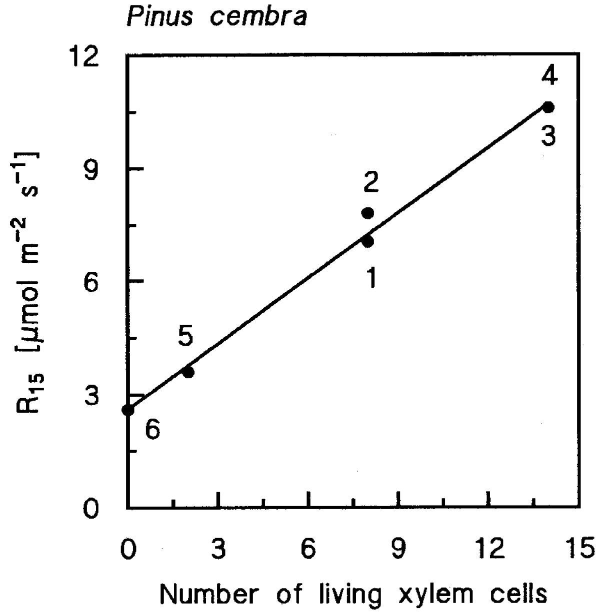

Fig. 6.15. Stem respiration normalised to 15 °C in relation to xylem production at breast height in an adult *Pinus cembra* tree. Xylem production is defined as the total number of living (newly built and lignifying) xylem cells. Measurements were made at Mt. Patscherkofel (Klimahaus), Austria, 1950 m a.s.l. in May (1), June (3), July (4), August (2), September (5), and October (6). (Modified after Havranek 1981.)

Havranek (1981) tried to check this observation and found a close correlation between *in situ* growing season stem respiration and the apparent number of living (i.e. newly built and lignifying) xylem cells with maintenance respiration left as the intercept on the y-axis when growth is zero (Fig. 6.15).

In contrast to foliage and woody-tissue respiration seasonal courses of fine root respiration have only been investigated in excavated roots of *Picea abies*, *Pinus cembra*, *Pinus mugo*, *Larix decidua* (Keller 1967) seedlings, and *Abies veitchii* saplings (Kimura et al. 1968). Available data so far show that at a reference temperature of 20 °C fine root respiration peaks in spring, tends to fall during the course of the growing season, and finally reaches a minimum during the winter. These observed high spring values have been attributed to a strong demand for carbohydrates in the buds just before and during the period of bud break (Kimura 1969; Harrasser 1976).

6.3 Carbon balance and allocation

6.3.1 The carbon balance

Carbon gain of a tree is determined from the assimilatory carbon uptake through the canopy (net photosynthesis of leaves) and the amount of carbon lost via autotrophic respiration. The decisive factor in carbon fixation is the time span over which a positive daily CO_2 balance is possible (*time factor*). Information about this period can be obtained by combining phenology and ecophysiology (Havranek and Tranquillini 1995). Measurements at the alpine timberline in the Central Tyrolean Alps (Ötztal, 2100 m a.s.l.) showed that the photosynthetic active (needle bearing) period for *Larix decidua* averaged over 6 years was 128 days (Friedel 1967). For comparison, daily mean air temperature was > 10 °C on 45 days and > 5 °C on 125 days, the latter closely matching the observed vegetation period. Conditions at the alpine timberline near Innsbruck (Klimahaus, Mt. Patscherkofel, 1950 m a.s.l.) appear to be similar: 46 days > 10 °C and 124 days > 5 °C. At this location the snow-free period averaged 168 ± 12 days and the period when air temperature was continuously > -4 °C was 165 ± 23 days, respectively (Havranek 1987). Both periods can be considered as an estimate for the time available to maintain a positive carbon gain in evergreen conifers, which is approximately 40 days more than the time available for the deciduous larch (Havranek and Tranquillini 1965).

The shorter photosynthetic season in *Larix* as compared to evergreen conifers can be compensated by a higher net photosynthetic capacity (see

Table 6.1), and hence also a higher daily and seasonal carbon gain (Tranquillini 1962). At the timberline on Mt. Patscherkofel (1950 m a.s.l.) needles of a mature *Larix decidua* accumulated 2.8 g carbon (C) per g needle dry weight within one growing season (Havranek unpublished 1982). This is approximately three times more than the annual net C gain estimated for *Pinus cembra* needles (0.9 g C per g needle dry weight; Wieser 2004a) at the same study site. Although the net yield of carbon assimilation was significantly higher in *Larix decidua* than in *Pinus cembra* (Table 6.4) the carbon use efficiency of the needles, i.e. the quotient of gross photosynthesis and respiration ($CUE_{leaf} = (P_n + R_d)/ R_d$; in terms of Larcher 2001) did not differ significantly between both species (Table 6.4).

Table 6.4. The annual carbon balance (mg C g_{dw}^{-1} $year^{-1}$) of *Larix decidua* and *Pinus cembra* needles. (After measurements from Havranek unpublished 1982 (*L. decidua*) and Wieser 2004a (*P. cembra*).)

	Larix decidua	*Pinus cembra*
Net photosynthetic yield	+ 2844	+ 895
Night-time respiration	- 427	- 149
Winter respiration	0	- 8
Annual total CO_2 balance	+ 2417	+ 738
Carbon use efficiency (growing season)	7.66	7.00
Carbon use efficiency (year)	7.66	6.68

At the tree level, the net carbon yield depends not only on the gas exchange intensity of the leaves, but also on the ratio of assimilating organs to that of respiring tissues (*structural factor*). Thus, canopy characteristics such as leaf development, leaf area, leaf area duration, and leaf mass influence the assimilatory carbon input of an entire tree. However, the rate of leaf area development in spring, although important in deciduous trees, is less important in evergreen conifers which retain their foliage for several years because new foliage comprises only a small fraction of the total leaf area (Gower et al. 1993).

A full seasonal carbon balance based on field measurements for an adult *Pinus cembra* tree at the alpine timberline on Mt. Patscherkofel near Innsbruck, Austria (1950 m a.s.l.) is shown in Fig. 6.16. Although CO_2 uptake is in general terminated during the winter at the alpine timberline (Tranquillini 1979), respiratory carbon losses during the dormant season do not burden the annual carbon balance. In *Pinus cembra* the daily carbon balance was negative for approximately five months (November up to mid April; Fig. 6.16) and it took a further month to compensate the total of 2.1 kg C lost by respiration during the dormant season (Fig. 6.16), which is 9 % of the annual carbon gain (Wieser et al. 2005).

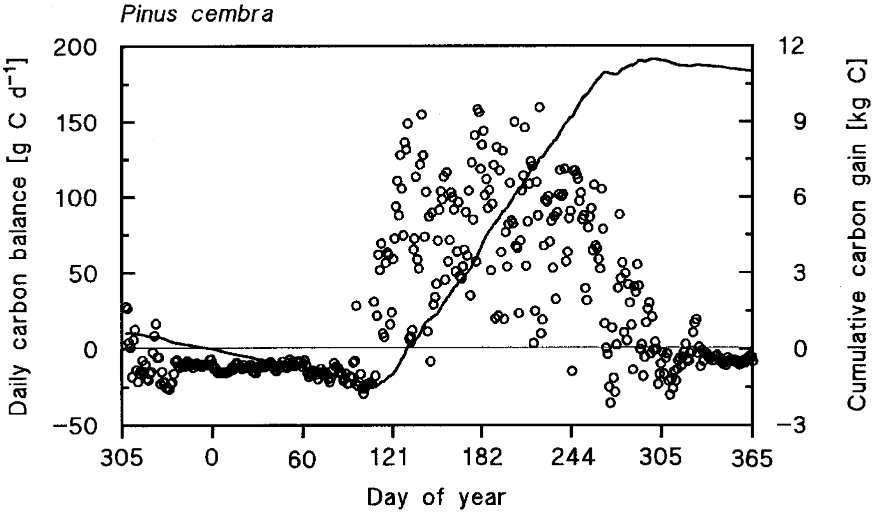

Fig. 6.16. The seasonal course of the daily carbon balance (open circles) and cumulative carbon gain (line) of a 95-year old *Pinus cembra* tree. Measurements were made at Mt. Patscherkofel (Klimahaus), Austria, 1950m a.s.l. Data are based on continuous chamber measurements of carbon fluxes from needles, branches, stem, and coarse roots combined with biomass determinations of the individual organs. (Modified after Wieser et al. 2005.)

During a five month dormancy total respiratory carbon losses of snow covered *Pinus cembra* seedlings was estimated to be about 7 % of the annual net carbon gain (Tranquillini 1959b). To compensate for this loss seedlings need to assimilate for three weeks after emergence from snow (Tranquillini 1979). For a mature *Larix decidua* tree respiration of the whole tree during the leafless period from October throughout April was calculated to be only 1.8 % of the annual net carbon gain (Havranek and Matyssek 2005). Hence, rather than being a burden the dormant season improves the tree's carbon balance because of a reduced respiration activity due to cold temperatures during the winter.

The annual carbon balance of an entire *Pinus cembra* (Wieser et al. 2005) and *Larix decidua* (Havranek and Matyssek 2005) tree at the alpine timberline on Mt. Patscherkofel near Innsbruck, Austria (1950 m a.s.l.) is shown in Table 6.5. The net photosynthetic yield of the adult *Pinus cembra* tree was 23.5 kg C per year as compared to 12.2 kg C estimated for a *Larix decidua* (Table 6.5). Total needle dry weight of the 70-year old and 8 m tall *Pinus cembra* tree was 25.7 kg, which is approximately 6 times the needle weight of 4.4 kg for *Larix decidua* similar in size and age. Similarly, Tranquillini and Schütz (1970) calculated a year round net photosynthetic carbon gain of 11.9 kg C for *Pinus cembra* (8.4 kg needle dry weight) and of 7.9 kg C for *Larix decidua* (3.4 kg needle dry weight). The superior performance in C uptake per leaf mass of *Larix decidua* can be attributed to a better interception of photosynthetic active radiation due to a more open crown when compared to *Pinus cembra*.

Table 6.5. The annual carbon budget of an adult *Pinus cembra* and *Larix decidua* tree at Mt. Patscherkofel (Klimahaus), Austria, 1950m a.s.l. (After Wieser et al. 2005 (*P. cembra*) and Havranek and Matyssek 2005 (*L decidua*).)

	Pinus cembra		*Larix decidua*	
NET PHOTOSYNTHESIS		100 % = 23570 g C $year^{-1}$		100 % = 12190 g C $year^{-1}$
RESPIRATION				
Needles	17.0		15.0	
Needle bearing twigs	1.4			
Branches	28.1		5.0	
Stem	6.0		14.0	
Coarse roots	4.5		4.0	
Total		57.0		38.0
GROWTH INCREMENT				
Needles	8.5		16.0	
Crrent shoot	3.2		2.0	
Branches	11.7		7.0	
Stem	7.6		14.0	
Coarse roots	4.5		4.0	
Total		35.0		43.0
FINE ROOTS and MYCORRHIZA		8.0		19.0

Total annual carbon loss respired by foliage and woody tissues was 57 and 38 % of the annual net photosynthetic carbon gain in *Pinus cembra* (Wieser et al. 2005) and *Larix decidua* (Havranek and Matyssek 2005), respectively (Table 6.5). This compares with 57 % for *Pinus contorta* and 43 % for *Nothofagus solandri* at a subalpine site in the Craigieburn Range, New Zealand (Benecke and Nordmeyer 1982). Kimura et al. (1968) estimated autotrophic respiration to comprise 40 % of the annual net carbon gain in young *Abies veitcii* trees at timberline on Mt Shimagare, Japan. These values estimated for trees at timberline are only 70 - 90 % of the annual carbon losses estimated for trees at lower, montane sites (Benecke and Nordmeyer 1982; Schulze et al. 1977; Schulze 1981).

In addition, carbon allocation into fine-root production (including respiratory losses and exudates to mycorrhiza) are remarkably small at the timberline (Table 6.6).This can be attributed to a low specific respiratory activity of the fine roots (cf. Table 6.3), cold root zone temperatures, and a supra-optimal soil water availability during the growing season. The latter is the key factor limiting total forest floor carbon efflux including autotrophic and heterotrophic respiration under current climatic conditions at the alpine timberline (Wieser 2004b).

Table 6.6. Percentages of annual growth increment allocated to organs for *Pinus cembra* (Wieser et al. 2005) and *Larix decidua* (Havranek and Matyssek 2005) on Mt. Patscherkofel, Austria, 1950 m a.s.l., as well as for *Pinus contorta* and *Nothofagus solandri* trees (Benecke and Nordmeyer 1982) in the Craigieburn Range, New Zealand, 1320 m a.s.l.

	Pinus cembra 95-year old	*Larix decidua* 65-year old	*Pinus contorta* 23-year old	*Nothofagus solandri* 52-year-old
Foliage	20	26	25	29
Branches	35	15	16	19
Stem	18	23	30	24
Coarse roots	9	6	8	8
Fine roots	19	31	21	20

Thus, the carbon use efficiency of timberline trees, expressed as the ratio of net primary production to photosynthetic carbon gain, ranges between 0.35 and 0.60, which is within the range of 0.30 and 0.65 reported for trees in boreal, temperate and tropical forest ecosystems (Saxe et al. 2001).

These data strongly suggest that the overall annual carbon budget of trees at timberline is balanced fairly well, and that trees at timberline are not burdened by a higher respiratory carbon loss than trees at lower elevation sites.

6.3.2 Carbon allocation

Allocation into structure - Net primary production

The surplus in the carbon balance, i.e. the amount of assimilated carbon not respired by foliage and woody tissues, increases the biomass of the tree and can be used for growth and accumulating reserves. On a proportionate basis trees at timberline allocate approximately 20 - 29 % into new foliage, 44 – 62 % into woody tissue (stem, branch, and coarse root biomass), and 19 - 31 % into fine roots (Table 6.6).

Although the annual fine root net primary production and total allocation of carbon to fine roots (including, respiration, and exudates to mycorrhizae; see surplus in Table 6.5) of trees at timberline is significantly above the mean value estimated for conifers in subtropic and warm temperate biomes (13 %), the mean rate of annual fine root net primary production in the timberline ecotone (23 %) is about 30 to 40 % lower than the mean rates of annual net primary fine root production reported for conifers in cold boreal (32 %) and temperate (37 %) climates, respectively (Gower et al. 1995).

There is also evidence that root growth is very sensitive to temperature. On a global scale, annual fine root growth increment and total carbon allocation to fine roots has been shown to be positively correlated to mean annual temperature (Gower et al. 1995). *In situ* observations on fine root growth in *Picea abies*, *Pinus cembra*, *Pinus mugo* (Turner and Streule 1983) and *Larix decidua* (Häsler et al. 1999) at the alpine timberline on Stillberg (Switzerland) showed that fine root growth ceases at root zone temperatures (≈ 10 cm soil depth) lower than 2 - 5 °C.

Root zone temperatures in the timberline ecotone of the European Alps remain continuously below 5 °C for more than 6 months and growing season maxima generally do not attain values above 15 °C (Hoch and Körner 2003; Körner and Paulsen 2004; Wieser 2004b). Thus, there is no doubt that a thermal limitation of the meristematic activity can be considered as the key factor for the observed limited fine root growth within the timberline ecotone.

No studies have attempted to quantify the amount of carbon allocated to mycorrhizae within the timberline ecotone to date. For an *Abies amabilis* stand in western Washington, 1150 m a.s.l. Vogt et al. (1982) estimated that 15 % of the total net primary production was allocated to fungi, including mycorrhizal-infected fine roots, although total fungi biomass contributed to less than 1 % of the total ecosystem biomass. However, despite the large amount of carbon allocated to mycorrhizae, they are essential for growth and survival of trees at timberline (cf. Chap. 4).

Although mycorrhization tends to decrease with increasing altitude (Read and Haselwandter 1981), it has been shown that the upper timberline in the central European Alps is exclusively formed by trees along with ectotrophic mycorrhizal symbionts (Göbl 1967; Moser 1967; Schinner 1978). Mycorrhization enables the trees to acquire sufficient resistance to adverse climatic constraints due to short and often unfavourable growing seasons in winter-cold mountains outside the tropics. Thus, in the opinion of Moser (1967) the upper limit of tree life designates the boundary above which the symbiosis of tree and ectotrophic fungi does no longer allow an adequate maturation of newly formed tissues. The latter would cause an enhanced vulnerability due to damages by winter desiccation, frost drought, freezing damage, and phototoxic effects.

Storage and reserve carbohydrates

In addition to carbon allocation into structural components some of the photosynthate is also allocated to a pool of mobile non-structural carbon compounds. This pool represents either storage or reserves and is composed of several compound classes (Chapin et al. 1990; Gower et al 1995). In trees within the timberline ecotone of the central European Alps, the two most important mobile carbon compounds are non-structural carbohydrates (starch, low molecular weight sugars) and lipids (acylglycerols) (cf. Hoch and Körner 2003; Hoch et al. 2003). Depending on the source-sink balance (net canopy photosynthesis versus carbon use for maintenance and growth) non-structural carbon compounds may either accumulate or decrease. Potential periods of carbon shortage in trees at the alpine timberline are the period of winter dormancy and the period of bud break and shoot elongation in spring when carbon demand exceeds carbon supply by photosynthesis (see Fig. 6.16).

Early investigations on the seasonal course of total mobile carbon compounds in *Abies veitchii* trees on Mt. Shimagare, Japan (2340 m a.s.l.) by Kimura (1969) indicated that mobile carbon compounds are highly abundant throughout an entire year and are never depleted significantly, neither in needles, branch, stem, and root wood (Fig. 6.17).

The largest fraction within the pool of total mobile carbon compounds were non-structural carbohydrates. At an average, annual mean lipid concentration accounted for 27, 48, 33, and 20 % for the estimated total amount of mobile carbon in needles, branches, stems, and roots, respectively. Furthermore, seasonal changes in the lipid fraction were relatively small, as also observed for *Pinus cembra* at the treeline in the Swiss Alps (Hoch et al. 2002; Körner 2003b), indicating that the major fraction of lipids is used for storage and not for seasonal growth.

Seasonal changes in starch appear to be similar in all tissues. In general, starch concentration within all tissue types is at low levels during the dormant season, and begins to accumulate just before the new growth begins in late spring (Kimura 1969) as shown for *Pinus cembra* needles in Fig. 6.18). Thus, expanding shoots are self-supporting, because carbon uptake starts prior to shoot growth (Wieser 1997), or they are fed by ongoing photosynthesis from older needles as shown for *Pinus sylvestris* at a low elevation site by Hansen and Beck (1994). During the growing season starch tends to exhibit a mid season depression (Hoch et al. 2002) and after having a second peak in autumn concentrations decrease to minimum levels of about 1 % in needles (Fig. 6.18) as also observed for woody tissues in young *Abies veitchii* trees on Mt. Shimagare, Japan (2340 m a.s.l.) by Kimura (1969).

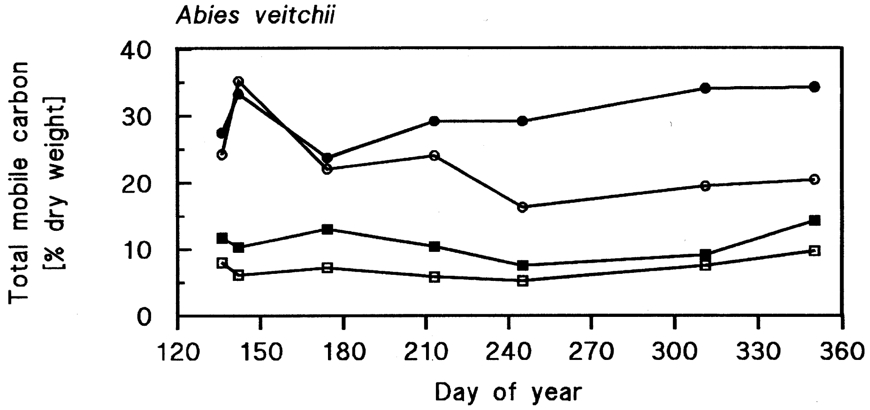

Fig. 6.17. Seasonal changes in total mobile carbon content (free sugars, starch, and lipids) in needles (•), branches (○), stems (■), and roots (□) of 15-year old *Abies veitchii* trees on Mt. Shimagare, Japan (2340 m a.s.l.). (Modified after Kimura 1969.)

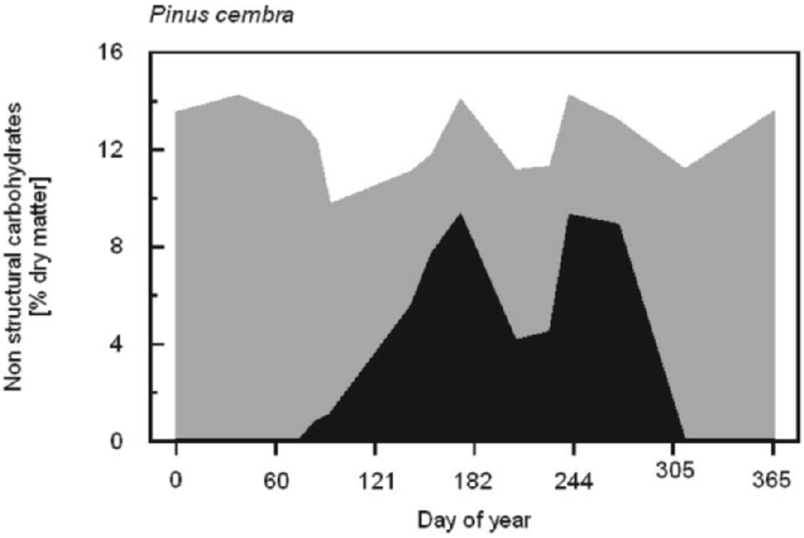

Fig. 6.18. Seasonal changes in non structural carbohydrates [free sugars (sucrose, glucose, and fructose; grey) and starch (black)] in *Pinus cembra* needles in the timberline ecotone of the European Alps (1950 – 2380 m a.s.l.). (Modified after Hoch et al. 2002; and Popp and Havranek unpublished 2003.)

Concentrations of free sugars (sucrose, glucose, and fructose) by contrast, are maintained at high levels during the cold season and are lowest during the growing season (Fig. 6.18; for all tree tissues see Kimura 1969). This accumulation of sugars prior and during the winter has shown to be associated with the development of freezing tolerance (Sakai and Larcher 1987; Havranek and Tranquillini 1995). In addition, Pisek et al. (1935) observed a late season increase in the osmotic potential in *Pinus cembra* needles at treeline in the Tyrolean Alps.

Ongoing research on the carbon charging of pines across the treeline ecotone in Mexico, the Swiss Alps, and northern Sweden (Hoch et al. 2002; Hoch and Körner 2003; Körner 2003b) reflect an altitudinal increase in the total amount of mobile carbon compounds with a maximum at the tree limit (Fig. 6.19). The latter however, can also be interpreted as an acclimation to high risks of tissue losses (Sveinbjörnsson 2000).

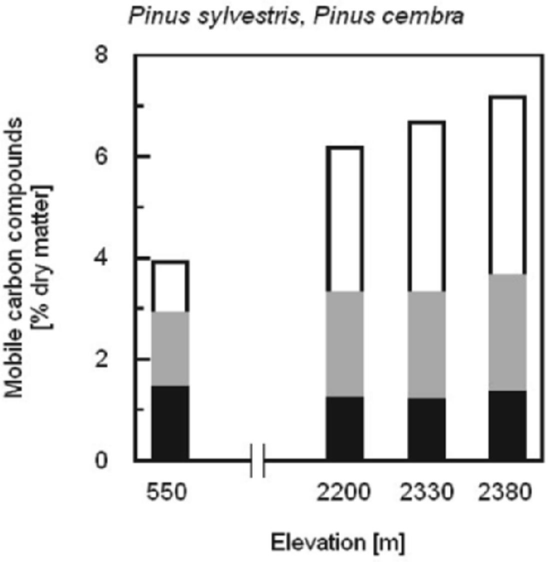

Fig. 6.19. Total above ground biomass low-molecular-weight sugar (black bars), starch (gray bars) and lipid (open bars) concentration (% dry mater) along an altitudinal transect in the Swiss Alps during the growing season. *Pinus sylvestris*, low altitude reference (550 m a.s.l.), *Pinus cembra* at the forest limit (2200 m a.s.l.), at an intermediate stand between the forest limit and the uppermost treeline (2330m a.s.l.), and at the uppermost treeline (2380 m a.s.l.). (Modified after Hoch and Körner 2003.)

Furthermore, *Pinus cembra* trees which were completely defoliated at the beginning of the growing season used up only 20-30 % of its total storage reserves in woody tissues for resprouting (Li et al. 2002). *In situ* exposure to elevated CO_2 (570 ppm) at the alpine timberline in the Swiss Alps induced an increase in non-structural carbohydrates of 7 and 37 % in the foliage of 30-year-old *Larix decidua* and *Pinus uncinata* trees, respectively after the first year of treatment (Hättenschwiler et al. 2002, Handa et al. 2005). Similar effects on non-structural carbohydrates were also observed in *Picea abies* seedlings growing in natural substrate and exposed to elevated CO_2 throughout three years in phytotrons (Körner 2003b). By contrast, in response to elevated CO_2 timberline trees showed no biomass increment, but an enhanced carbon allocation into roots, and thus leading to a significant reduction in needle mass and leaf area (Hättenschwiler and Körner 1998). Thus, enhanced contents of mobile carbohydrates in needles might have signalled a restricted carbon demand and thus causing a down-regulation of carbon uptake at the canopy level (cf. also Wiemken and Ineichen 2000).

Taken together, a highly positive carbon balance combined with the continuous high abundance of mobile carbon compounds in trees growing in the timberline ecotone can not fully explain the upper limit of tree life in the temperate zone. However, what remains to be taken into account is that the upper limit of tree life might be attributed to a massive imbalance in the ratio of photosynthesizing foliage versus respiring tissues. Thus, dry matter allocation rather than carbon gain might be the critical factor. This is because the latter strongly depends on allometric traits such as leaf mass ratio (LMR, leaf mass versus total tree biomass) and root mass ratio (RMR, root mass versus total tree biomass).

6.4 Carbon accumulation of trees in the timberline ecotone

6.4.1 Dry matter accumulation patterns

Unfortunately, dry matter accumulation patterns are poorly documented for timberline trees. 23-year old *Larix decidua*, *Pinus cembra*, and *Pinus uncinata* trees at the Swiss treeline near Davos (2080 to 2200 m a.s.l.) accumulate 7 (deciduous) to 16 % (evergreen) into needles (LMR) and 11 to 14 % into roots (RMR), respectively (Bernoulli and Körner 1999). For trees of similar age at the alpine timberline on Mt. Patscherkofel, Austria (1950 m a.s.l.) Framba (1980) found a LMR of 36 % in *Pinus cembra* and even 42 % in *Picea abies*. Corresponding RMR were 18 and 16 %, respectively.

Total tree biomass of even aged *Pinus cembra* (Fig. 6.20), *Pinus uncinata*, and *Larix decidua* trees showed no elevational trend across the timberline ecotone (Oswald 1963; Bernoulli and Körner1999). Elevational trends in accumulation patterns also do not exist in *Larix decidua*, but a significant increase in the leaf mass ratio was observed in *Pinus cembra* and *Pinus uncinata* from about 10 % at the lower end to round 20% at the upper end of a 140 m elevational transect across the treeline ecotone in the Swiss Alps (Bernoulli and Körner 1999).

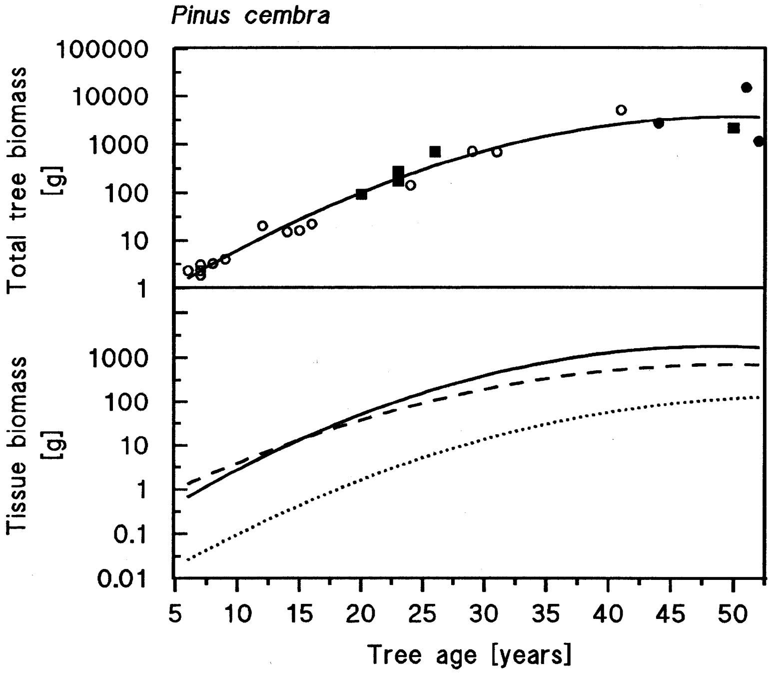

Fig. 6.20. **(top)** Total tree biomass for a *Pinus cembra* chronosequence in the timberline ecotone near Obergurgl, Austria between 1985 to 2194 m a.s.l. **(bottom)** Relations developed for *Pinus cembra* showing that stem and branch (solid line), coarse roots (hatched line), and needle biomass (dotted line) increase exponentially with tree age. Lines were fit by the following regressions: stem and branch wood: log y = (-0.004*x+0.42)*x-2.76; coarse roots: log y = (-0.003*x+0.32)*x-1.54; needles: log y = (-0.003*x+0.39)*x-5.80. Trees were excavated at 1985 (○, forest limit), at 2145 (•, lower timberline ecotone), and at 2194 m elevation (■, upper timberline ecotone). (Modified after Tranquillini 1959b; and Oswald 1963.)

Similarly, Oswald (1963) observed a significant increase in the leaf mass ratio from 18 to 28 % in 24 to 52 year-old *Pinus cembra* trees along an elevational transect from the upper limit of the closed forest at 1985 m a.s.l. up to the *kampfzone* in the upper timberline ecotone at 2194 m a.s.l. (Table 6.7). In parallel, the total amount of carbon allocated to branches increases when approaching the upper limit of tree growth, while the opposite was found for carbon allocation into the stem (Table 6.7).

Table 6.7. Relative changes in needle, branch, stem, and root biomass allocation ratios for 20 to 52-year old *Pinus cembra* trees across an elevational gradient at the timberline ecotone near Obergurgl, Austria, 1985 to 2194 m a.s.l. (After Oswald 1963.)

Elevation [m]	Age [years]	Needles [%]	Branches [%]	Stem [%]	Roots [%]
1985	24-41	18	10	41	31
2145	44-52	19	18	33	30
2194	20-50	27	28	22	23

Consequently tree height declines significantly by 20 (*Larix decidua*) to 50 % (*Pinus cembra*, *Pinus uncinata*) per 100 m of elevation (Oswald 1963; Bernoulli and Körner 1999; Paulsen et al. 2000). Thus, trees develop a more stunted morphology (Tranquillini 1979) which enables them to spread their autotrophic foliage closer to the soil surface where thermal conditions are more favourable than in the free atmosphere.

6.4.2 Changes in carbon accumulation with tree age

As long as trees grow, there is an increase in biomass and carbon accumulation in stem and branch wood, coarse roots, and foliage increases exponentially with tree age (cf. Fig. 6.20). Factors directly controlling carbon allocation patterns in individual trees remain largely unknown, and include genetic, biochemical, physiological source sink regulations (Gower et al. 1995), and competition among trees (Nilsson and Albrekstson 1993). Carbon allocation to the stem raises the tree's canopy above competitors. Allocation to foliage depends in part on the availability of resources at a given site, such as water and nutrients. Resource acquisition on the other hand depends on allocation patterns into fine roots and mycorrhizae.

Nevertheless, carbon allocation and accumulation patterns change as trees age, as shown in an age sequence for *Pinus cembra* in Fig. 6.21. On a relative scale, young trees accumulate more carbon into foliage than into above and below ground woody tissue.

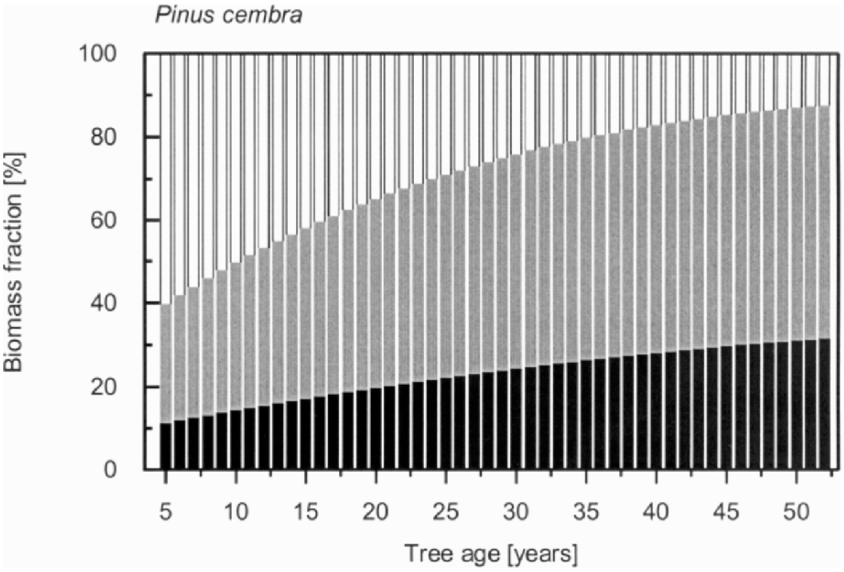

Fig. 6.21. Relative changes in foliage (open bars), stem, branch (grey bars), and coarse root (black bars) carbon accumulation patterns with tree age in *Pinus cembra* at the timberline ecotone near Obergurgl, Austria. (Modified after Tranquillini 1959b and Oswald 1963.)

This ratio continuously declines with increasing tree age and comes close to 15 % in 50 (Fig. 6.21) to 95-year-old trees (Wieser et al. 2005). Carbon accumulation into above ground woody tissues and coarse roots by contrast, increases with tree age (Fig. 6.21) and approach 60 and 25 %, respectively in trees older than 50 years (Wieser et al. 2005).

This imbalance in carbon accumulation of foliage versus respiring tissues is the basis for the often cited (but not tested) hypothesis that an imbalance between carbon uptake and loss might limit tree growth at the alpine treeline (Körner 2003a, b). However, in trees much of the above and below ground woody-biomass is metabolically inactive, suggesting that a relatively high fraction of heterotrophic tissues is not necessarily critical for the carbon balance of trees at the alpine treeline.

On the other hand, the increasing imbalance in carbon accumulation patterns into autotrophic and heterotrophic tissue with increasing tree age might probably burden the overall carbon balance the older the trees are. Direct measurements and calculations of the annual carbon balance argue in this direction. Based on field measurements, the annual carbon gain in *Pinus cembra* declines from 77 % of the annual net photosynthetic carbon yield in 7 year-old seedlings (Tranquillini 1959b) to 43 % in a 95-year-old tree (Wieser et al. 2005). Using published gas exchange data (Tranquillini 1959b; Tranquillini and Schütz 1970; Havranek 1981; Wieser et al. 2004) and whole tree biomass accumulation patterns from a chronosequence (Tranquillini 1959b; Oswald 1963; cf. also Fig. 6.21) for estimating the annual dry matter production yields similar results. Extrapolating these results suggest that the carbon gain of *Pinus cembra* at the alpine timberline may approach zero when trees are older than 3000 years (Fig. 6.22).

The existence of several thousand year old *Pinus aristata* and *Pinus longaeva* trees at the upper timberline in North American mountain ranges (White Mountains, Snake Range, Front Range) also suggest that even a marginal carbon balance does not limit tree growth, as there is evidence that these trees survived periods with climatic conditions less favourable for maintaining a positive annual carbon balance than under present climatic conditions (Arno 1984).

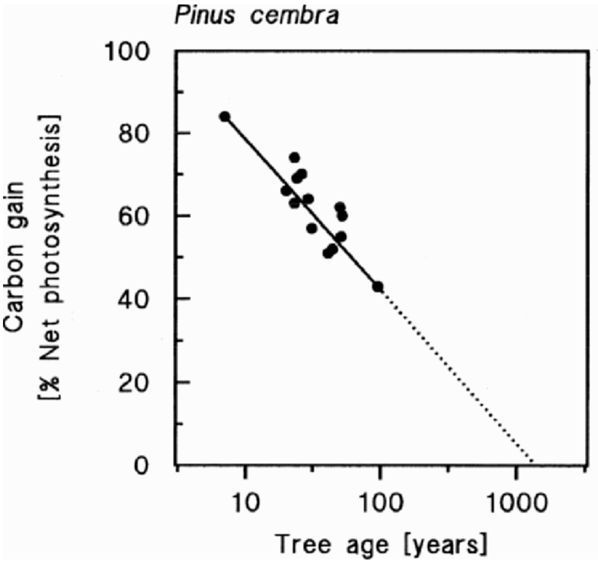

Fig. 6.22. Proposed decline in the annual carbon gain with increasing tree age in *Pinus cembra* trees, based on gas exchange measurements Tranquillini (1959b; Wieser et al. 2005) and biomass data obtained from Fig. 6.20 (Tranquillini 1959b; and Oswald 1963). Points were fit by linear regression (solid line): y=-30*(log x)+107, r^2=0.79.

6.5 Net ecosystem production at timberline

Net ecosystem CO_2 exchange is the small difference between gross primary production (GPP; or carbon assimilated by the canopy) and total ecosystem respiration (ER) as the sum of autotrophic and heterotrophic respiration. On an annual basis, undisturbed forest ecosystems generally show a small net gain in the carbon exchange with the atmosphere (Waring and Running 1998), and thus representing net ecosystem production (NEP) or carbon sequestration. To estimate net carbon uptake through photosynthesis and to separate ecosystem respiration into various components a series of chambers can be installed on the soil, coarse roots, the stem, branches, and the foliage (Waring and Running 1998; Larcher 2001). In addition, the proportions by mass of all the different organs have to be determined for up-scaling. Eddy-flux installations are an alternative approach, but this method is strongly limited in heterogeneous and mountainous landscapes such as the timberline ecotone (cf. Zeller and Nikolov 2000).

In the timberline ecotone of the central European Alps net ecosystem CO_2 exchange dynamics have only been estimated for a 95-year-old *Pinus cembra* forest with a stand density of 1038 trees ha^{-1}, a basal area of 47.6 m^2 ha^{-1}, and a projected leaf area index of 3.9 m^2 m^{-2} (Wieser and Stöhr 2005). In this forest daily net ecosystem production varied between -3.0 g C m^{-2} ground surface area d^{-1} during the winter and 9.9 g C m^{-2} d^{-1} during the growing season. Gross primary production and ecosystem respiration had similar trends as net ecosystem production, with maximum values up to 14.9 and 11.1 g C m^{-2} ground surface area d^{-1} (Fig. 6.23).

Annual gross primary production of this open *Pinus cembra* forest yielded 1610 g C m^{-2} ground surface area $year^{-1}$ (Table 6.8), which is within the range of 831 to 1691 g C m^{-2} $year^{-1}$ estimated for other high altitude and high latitude coniferous forests (Valentini et al. 2000; Falge et al. 2002; Zha et al. 2004). Total annual ecosystem respiration was 1247 g C m^{-2} $year^{-1}$ and was composed of the following component fluxes: 22 % from the foliage, 68 % from branches, 4 % from stems, 4 % from coarse roots, 2 % from small roots (diameter < 5 mm), and 1 % from heterotrophic components (Table 6.8). These low carbon efflux rates from all the below ground components of the ecosystem (Table 6.8) can be attributed to low root zone temperatures (Wieser and Bahn 2004) as well as to a supra-optimal soil water availability, because soil water potentials and volumetric soil water contents exceeding -0.03 MPa and 55 m^3 m^{-3}, respectively significantly depressed soil surface CO_2 efflux (Wieser 2004b) in this haplic podzol, a soil type typical for the timberline ecotone in the central Austrian Alps (Neuwinger 1970, 1980).

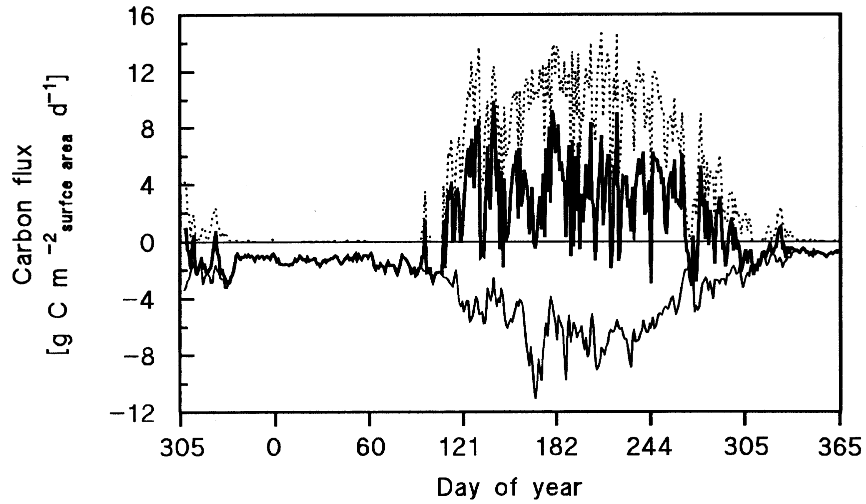

Fig. 6.23. The seasonal time course of net ecosystem production (thick solid line), ecosystem respiration (thin solid line), and gross primary production (dotted line) of a 95-year old *Pinus cembra* forest. Measurements were made at Mt. Patscherkofel (Klimahaus), Austria, 1950m a.s.l. (After Wieser and Stöhr 2005.)

Table 6.8. Annual gross primary production, ecosystem respiration, component respiration and annual net ecosystem production of a 95-year-old *Pinus cembra* forest. Measurements were made at Mt. Patscherkofel (Klimahaus), Austria, 1950m a.s.l. (After Wieser and Stöhr 2005.)

	g C m^{-2} ground surface area year^{-1}	%
GROSS PRIMARY PRODUCTION	1610	100.0
ECOSYSTEM RESPIRATION	1247	77.5
Foliage respiration	276	17.1
Branch respiration	847	52.5
Stem respiration	45	2.8
Coarse root respiration	50	31.
Small root respiration	22	1.4
Heterotrophic respiration	11	0.7
NET ECOSYSTEM PRODUCTION	363	22.5

Net ecosystem production of this forest ecosystem was 363 g C m^{-2} year^{-1} which is within the range reported for other high elevation coniferous forest ecosystems (58 to 500 g C m^{-2} year^{-1}) in the Snowy Mountains, Wyoming (Zeller and Nikolov 2000) and in the Front Range, Colorado, USA (Carey et al. 2001; Monson et al. 2002). In a study on net ecosystem production in forest ecosystems across a latitudinal transect in Europe, Valentini et al. (2000) reported values ranging from 470 to 600 g C m^{-2} year^{-1} at latitudes lower than 51° N and values from -80 to 245 C m^{-2} year^{-1} at higher latitudes, clearly indicating that the length of the growing period and hence also temperature strongly affects net ecosystem production.

The ratio of net ecosystem production to gross primary production (= carbon use efficiency in terms of Saxe et al. 2001) in this forest ecosystem at the alpine timberline in the central European Alps was 0.23, which is within the mean range reported for forest of the temperate zone (0.28 ± 0.10) but significantly above the range reported for boreal forests (0.17 ± 0.12) by Falge et al. (2002).

Throughout the growing season (cf. Fig. 6.23) when net carbon uptake was not limited by cold temperatures, the temperature response curve of gross primary production is relatively wide (Fig. 6.24).

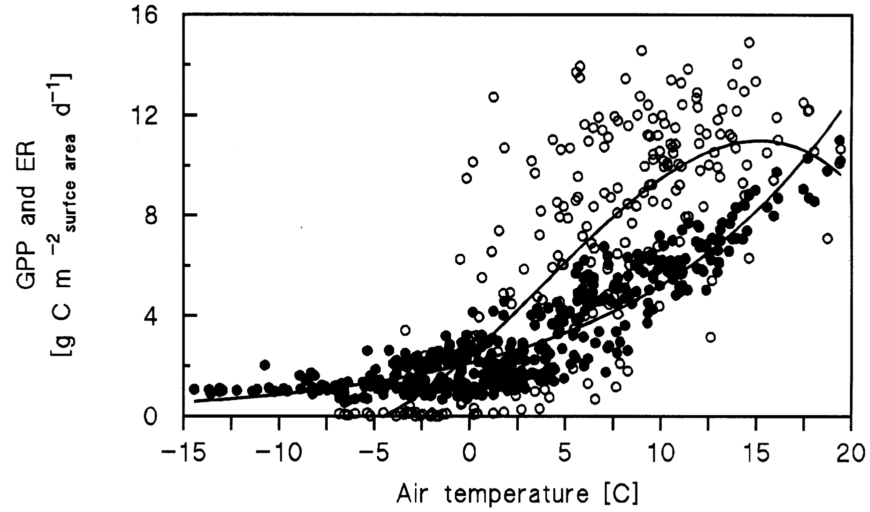

Fig. 6.24. Gross primary production during the growing season (GPP, open circles) and year round ecosystem respiration (ER, closed circles) in relation to air temperature in a 95-year old *Pinus cembra* forest. Measurements were made at Mt. Patscherkofel (Klimahaus), Austria, 1950m a.s.l. (Modified after Wieser and Stöhr 2005.)

This is because net photosynthesis of conifers within the timberline ecotone operates at more than 90 % of its maximum at a temperature range between 5 and 20 °C (cf. also Figs. 6.7 and 6.12). Ecosystem respiration by contrast, increased exponentially with air temperature (Fig. 6.24).

Thus, the relationships observed for gross primary production and ecosystem respiration (Fig. 6.24) strongly suggest that, under current climatic conditions warm temperatures during the growing season (see Figs. 6.9, 6.12, and 6.14) and their effects on ecosystem respiration (Fig. 6.24) are the key factors limiting net ecosystem production in forest ecosystems within the timberline ecotone of the central European Alps (Wieser and Stöhr 2005), as also observed in a subalpine forest (3050 m a.s.l.) at the Niwot Ridge, USA (Huxman et al. 2003). Low temperatures by contrast are not necessarily a burden to the overall carbon sequestration of high elevation forest ecosystems.

Taken together, data presented in this chapter do not support the hypothesis that either an insufficient carbon uptake during the growing season or the balance between uptake and loss of carbon is insufficient for supporting maintenance and primary production of trees and even forest ecosystems within the timberline ecotone of the central European Alps. In addition, the significant large fraction of heterotrophic tissues of total tree biomass is also not critical for the overall carbon balance in the timberline ecotone. Thus, the carbon limitation hypothesis does not provide the answer for explaining the upper limit of tree life in the temperate zone.

References

Arno MF (1984) Timberline: mountain and arctic forest frontiers. The Mountaineers, Seattle

Bauer H, Huter M, Larcher W (1969) Der Einfluß und die Nachwirkung von Hitze und Kältestress auf den CO_2-Gaswechsel von Tanne und Ahorn. Berichte der deutschen Botanischen Gesellschaft 82: 65-70

Benecke U, Havranek WM (1980) Gas exchange of trees at altitudes up to timberline, Craigieburn Range, New Zealand. In: Benecke U, Davies MD (eds) Mountain environments and subalpine tree growth. New Zealand Forest Service, Technical Report 70, pp 195-212

Benecke U, Nordmeyer AH (1982) Carbon uptake and allocation by *Nothofagus solandri* var. *cliffortoides* (hook. F.) Poole and *Pinus contorta* Douglas ex Loundon ssp. *contorta* at montane and subalpine altitudes. In: Waring RH (ed) Carbon uptake and allocation in subalpine ecosystems as a key to management. Proceedings of an IUFRO Workshop, Forest Research Laboratory, Oregon State University, Corvallis, Oregon, pp 9-21

Benecke U, Schulze E-D, Matyssek R, Havranek WM (1981) Environmental control of CO_2-assimilation and leaf conductance in *Larix decidua* Mill. I. a comparison of contrasting natural environments. Oecologia 50: 54-61

Bernoulli M, Körner Ch (1999) Dry matter allocation in treeline trees. Phyton 39: 7-12

Bolhar-Nordenkampf H, Lechner EG (1989) Saisonale und streßbedingte Modifikationen der photosynthetischen Kapazität von Fichten im Höhenprofil "Zillertal". Phyton 29: 207-227

Boysen-Jensen P (1932) Die Stoffproduktion der Pflanzen. Fischer Jena

Cairns DM (1998) Modelling controls on pattern at alpine treeline. Geographical and Environmental Modelling 2: 43-64

Cairns DM, Malanson GP (1998) Environmental variables influencing the carbon balance at the alpine treeline: a model approach. Journal of Vegetation Science 9: 697-692

Caldwell MM (1970a) The effect of wind on stomatal aperture, photosynthesis, and transpiration of *Rhododendron ferrugineum* L. and *Pinus cembra* L. Centralblatt für das Gesamte Forstwesen 87: 193-201

Caldwell MM (1970b) Plant gas exchange at high wind speeds. Plant Physiology 46: 535-537

Carey EV, Sala A, Keane R, Callaway RM (2001) Are old forests underestimated as global carbon sinks? Global Change Biology 7: 339-344

Cartellieri E (1935) Jahresgang von osmotischem Wert, Transpiration und Assimilation einiger Ericaceen der alpinen Zwergstrauchheide und von *Pinus cembra*. Jahrbücher für wissenchaftliche Botanik 82: 460-506

Chapin FS, Schulze E-D, Mooney HA (1990) The ecology and economics of storage in plants. Annual Review of Ecology and Systematics 21: 423-447

Cowan IR (1977) Stomatal behaviour and envirinment. Advances in Botanical Research 4: 177-228

Dang QL, Margolis HA, Coyea MR, Sy M, Collatz GJ (1997) Regulation of branch-level gas exchange of boreal trees: roles of shoot water potential and vapour pressure difference. Tree Physiology 17: 521-535

Eccher M (1972) Die Wurzelatmung von Holzpflanzen und ihre Bedeutung für die Stoffproduktion. Diploma thesis, Innsbruck University

Ellenberg H (1975) Vegetationsstufen in perhumiden bis perariden Bereichen der tropischen Anden. Phytocoenologia 2: 368-387

Falge E, Baldocchi D, Tehnunen J, Aubinet M, Bakwin P, Berbigier P, Bernhofer Ch, Bonnefond J-M, Burba G, Clement R, Davis KJ, Elbers JA, Falk M, Goldstein AH, Grelle A, Granier A, Grünwald T, Goumundsson J, Hollinger D, Janssens IA, Keronen P, Kowalski AS, Katul G, Law BE, Malhi Y, Meyers T, Monson RK, Moors E, Munger JW, Oechel W, Pawu KT, PIlegraad K, Rannik U, Rebmann U, Suyker A, Thorgeirsson H, Tirone G, Turnipseed A, Wilson K, Wolfsy S (2002) Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. Agricultural and Forest Meteorology 113: 57-74

Farquhar GD (1978) Feedforward responses of stomata to humidity. Australian Journal of Plant Physiology 5: 787-800

Fliri F (1975) Das Klima der Alpen im Raume von Tirol. Monographien zur Landeskunde Tirols I. Universitätsverlag Wagner, Innsbruck, München

Framba L (1980) Beiträge zur Methodik der Wurzelatmungsmessung und ihre Anwendung bei der physiologischen Charakterisierung von jungen Nadelbäumen. Ph.D. thesis, Innsbruck University

Friedel H (1967) Verlauf der alpinen Waldgrenze in Rahmen anliegender Gebirgsgelände. Mitteilungen Forstliche Bundesversuchsanstalt Mariabrunn 59: 81-172

Friend AL, Coleman MD, Isebrands JG (1994) Carbon allocation to root and shoot systems of woody plants. In: Davis TD, Haissing BE (eds) Biology of adventitious root formation. Plenum Press, New York, pp 245-273

Gansert D, Backes K, Ozaki T, Kakubari Y (2002) Seasonal variation of branch respiration of a treeline forming (*Betula ermanii* Cham.) and a montane (*Fagus crenata* Blume) deciduous broad-leaved tree species on Mt. Fuji, Japan. Flora 197: 186-202

Göbl F (1967) Mykorrhizauntersuchungen in subalpinen Böden. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 65: 335-356

Gonzales-Rodríguez AM, Morales D, Jiménez MS (2001) Gas exchage characteristics of a Canarian laurel forest tree species (*Laurus azoica*) in relation to environmental conditions and leaf canopy position. Tree Physiology 21: 1039-1045

Gower ST, Reich PB, Son Y (1993) Canopy dynamics and above ground production for five tree species with different leaf longevities. Tree Physiology 12: 327-345

Gower ST, Isebrands JG, Sheriff DW (1995) Carbon allocation and accumulation in conifers. In: Smith WJ, Hinckley TM (eds) Resource physiology of conifers: acquisition, allocation and utilisation. Academic Press, San Diego, pp 217-254

Gross M (1989) Untersuchungen an Fichten der alpinen Waldgrenze. Dissertationes Botanicae 119. Cramer, Berlin, Stuttgart

Guggenberger H (1980) Untersuchungen zum Wasserhaushalt der alpinen Zwergstrauchheide Patscherkofel. Ph.D. thesis, Innsbruck University

Gunsch J (1972) Vergleichende ökologische Untersuchungen von Kleinstandorten im Bereich der subalpinen Zirben-Waldgrenze. Ph.D. thesis, Innsbruck University

Hadley JL, Smith WK (1987) Influence of krummholz mat microclimate on needle physiology and survival. Oecologia 73: 82-90

Handa T, Körner Ch, Hättenschwiler S (2005) A test of the treeline carbon limitation hypothesis by in situ CO2 enrichment and defoliation. Ecology 86: 1288-1300

Hansen J, Beck E (1994) Seasonal changes in the utilization and turnover of assimilation products in 8-year-old Scots pine (*Pinus sylvestris*) trees. Trees 8: 172-182

Harrasser P (1976) Der Jahresgang des Wurzelatmungsvermögens von Fichten, Zirben und Lärchen. Mit einem Beitrag zur Methodik der Wurzelatmungsmessung. Ph.D. thesis, Innsbruck University

Häsler R (1994) Ecophysiological investigations on cembran pine at timberline in the Alps, an overview. In: Schmidt WC, Holtmeier F-K (eds) Proceedings – International workshop on subalpine stone pines and their environment: the status of knowledge; Sept. 5-11; St. Moritz, Switzerland. Tech. Rep. INT-GTR-309. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT, pp. 61-66

Häsler R, Savi C, Herzog K (1991) Photosynthese und stomatäre Leitfähigkeit der Fichte unter dem Einfluss von Witterung und Luftschadstoffen. In: Stark M (ed) Luftschadstoffe und Wald. Verlag der Fachvereine, Zürich, pp 143-168

Häsler R, Streule A, Turner H (1999) Shoot and root growth of young *Larix decidua* in contrasting environments near the alpine timberline. Phyton 39: 47-52

Hättenschwiler S, Körner Ch (1998) Biomass allocation and canopy development in spruce model ecosystems under elevated CO_2 and increased N deposition. Oecologia 113: 104-114

Hättenschwiler S, Handa IT, Egli L, Asshoff R, Ammann W, Körner Ch (2002) Atmospheric CO_2 enrichment of alpine timberline conifers. New Phytologist 156: 365-375

Havranek WM (1972) Über die Bedeutung der Bodentemperatur für die Photosynthese und die Transpiration junger Forstpflanzen und für die Stoffproduktion an der Waldgrenze. Angewandte Botanik 46: 101-116

Havranek WM (1981) Stammatmung, Dickenwachstum und Photosynthese einer Zirbe (*Pinus cembra*) an der Waldgrenze. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 142: 443-467

Havranek WM (1985) Gas exchange and dry matter allocation in larch at the alpine timberline. In: Turner H, Tranquillini W (eds) Establishment and tending of subalpine forest: research and management. Eidgenössische Anstalt für das Forstliche Versuchswesen, Ber. 270, pp 135-142

Havranek WM (1987) Physiologische Reaktionen auf Klimastreß bei Bäumen an der Waldgrenze. GSF Bericht 10/87: 115-130

Havranek WM, Benecke U (1978) The influence of soil moisture on water potential, transpiration and photoynthesis of conifer seedlings. Plant and Soil 49: 91-103

Havranek WM, Matyssek R (2005) The carbon balance of European larch (*Larix decidua*) at the alpine timberline. Phyton 45:213-231

Havranek WM, Tranquillini W (1995) Physiological processes during winter dormancy and their ecological significance. In: Smith WK, Hinckley TM (eds) Ecophysiology of coniferous forests. Academic Press, San Diego, pp 95-124

Havranek WM, Wieser G (1993) Zur Ozontoleranz der Lärche (*Larix decidua* Mill.). Forstwissenschaftliches Centralblatt 112: 56-64

Hoch G, Körner Ch (2003) The carbon charging of pines at the climatic treeline: a global comparison. Oecologia 135: 10-21

Hoch G, Popp M, Körner Ch (2002) Altitudinal increase of mobile carbon pools in *Pinus cembra* suggests sink limitation of growth at the Swiss treeline. Oikos 98: 361-374

Hoch G, Richter A, Körner Ch (2003) Non-structural carbon compounds in temperate forest trees. Plant, Cell and Environment 26: 1067-1081

Hollinger DY (1989) Canopy organisation and foliage photosynthetic capacity in a broad-leaved evergreen montane forest. Functional Ecology 3: 52-62

Hurtin KR, Marshall JD (2000) Altitude trends in conifer leaf morphology and stable carbon isotope composition. Oecologia 123: 32-40

Huxman TE, Turnipseed AA, Sparks JP, Harley PC, Monson RK (2003) Temperature as a control over ecosystem CO_2 fluxes in a high-elevation, subalpine forest. Oecologia 134: 537-546

Jones HG (1991) Plants and microclimate. A quantitative approach to environmental plant physiology. University Press, Cambridge

Kaiser WM (1987) Effects of water deficit on photosynthetic capacity. Physiologia Plantarum 77: 142-149

Keller T (1967) Beitrag zur Kenntnis der Wurzelatmung von Koniferenjungpflanzen. Proc. 14th IUFRO Congress. Munich IV, Sect. 23: 329-340

Kimura M (1969) Ecological and physiological studies on the vegetation of Mt. Shimagare. VII. Analysis of production processes of a young *Abies* stand based on the carbohydrate economy. Botanical Magazine Tokyo 82: 6-19

Kimura M, Monotiani I, Hogsetu K (1968) Ecological and physiological studies on the vegetation of Mt. Shimagare. VI. Growth and dry matter production of a young *Abies* stand. Botanical Magazine Tokyo 81: 287-296

Koike T, Häsler R, Item H (1994) Needle longevity and photosynthetic performance in cembran pine and Norway spruce growing on the north- and east-facing slopes at the timberline of Stillberg in the Swiss Alps. In: Schmidt WC, Holtmeier F-K (eds) Proceedings – International workshop on subalpine stone pines and their environment: the status of knowledge; Sept. 5-11; St. Moritz, Switzerland. Tech. Rep. INT-GTR-309. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT, pp 78-80

Körner Ch (1994) Leaf conductance in the major vegetation types of the globe. In: Schulze E-D, Caldwell MM (eds) Ecophysiology of photosynthesis. Ecological Studies, vol 100. Springer, Berlin, Heidelberg, New York, pp 463-490

Körner Ch (2003a) Alpine plant life: functional plant ecology of high mountain eosystems. 2nd edn. Springer Berlin, Heidelberg, New York

Körner Ch (2003b) Carbon limitation in trees. Journal of Ecology 94: 4-17

Körner Ch, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. Journal of Biogegraphy 31: 713-732

Larcher W (1961) Jahresgang des Assimilations- und Respirationsvermögens von *Olea europea* L. ssp. *sativa* Hoff. Et Link., *Quercus ilex* L. und *Quercus pubescens* Wild. aus dem nördlichen Gardaseegebiet. Planta 56: 557-606

Larcher W (2001) Ökophysiologie der Pflanzen: Leben, Leistung und Stressbewältigung der Pflanzen in ihrer Umwelt. Ulmer, Stuttgart

Li MH, Hoch G, Körner Ch (2002) Source/sink removal affects mobile carbohydrates in *Pinus cembra* at the Swiss treeline. Trees 16: 331-337

Markart G (2000) Der Wasserhaushalt von Hochlagenaufforstungen. Schriftenreihe der Forstlichen Bundesversuchsanstalt Wien, FBVA-Bericht 117

Martin TA, Hinckley TM, Meinzer FC, Sprugel DG (1999) Boundary layer conductance, leaf temperature and transpiration of *Abies amabilis* branches. Tree Physiology 19: 435-443

Matyssek R (1985) The carbon balance of three deciduous larch species and an evergreen spruce species near Bayreuth (W.-Germany). In: Turner H, Tranquillini W (eds) Establishment and tending of subalpine forest: research and management. Eidgenössische Anstalt für das Forstliche Versuchswesen, Ber. 270, pp 123-133

McLaughlin SB, Andersen CP, Hanson PJ, Tjoelker MG, Roy WK (1991) Increased dark respiration and calcium deficiency of red spruce in relation to acidic deposition at high-elevation southern Appalachian Mountain sites. Canadian Journal of Forest Research 21: 1234-1244

Monson RK, Turnipseed AA, Sparks JP, Harley PC, Scott-Denton LE, Sparks K, Huxman TE (2002) Carbon sequestration in a high-elevation, subalpine forest. Global Change Biology 8: 459-478

Mooney HA, Wright RD, Strain BR (196). The gas exchange capacity of plants in relation to vegetation zonation in the White Mountains of California. The American Midland Naturalist 72: 281-297

Morales D, Gonzales-Rodriguez AM, Cermak J, Jimenez MS (1996) Laurel Forest in Tenerife, Canary islands: the vertical profiles of leaf characteristics. Phyton 36: 251-263

Moser M (1967) Die ektotrophe Ernährungsweise an der Waldgrenze. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 65: 357-375

Nagele M (1989) Veränderungen der Photosyntheseaktivität ausgewählter Holzpflanzen. Ph.D. thesis, Innsbruck University

Neuwinger I (1970) Böden der subalpinen und alpinen Stufe in den Tiroler Alpen. Mitteilungen der Ostalpin-Dinarischen Gesellschaft 11: 135-150

Neuwinger I (1980) Erwärmung, Wasserrückhalt und Erosionsbereitschaft subalpiner Böden. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 129: 113-144

Neuwinger-Raschendorfer I (1961) Bodenfeuchtemessungen. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 257-264

Niinemets U, Oja V, Kull O (1999) Shape of leaf photosynthetic electron transport versus temperature response curve is not constant along canopy light gradients in temperate deciduous trees. Plant, Cell and Environment 22: 1497-1513

Nilsson U, Albrekstson A (1993) Productivity of needles and allocation of growth in young Scots pine trees of different competitive status. Forest Ecology and Management 62: 173-187

Oren R, Schulze E-D, Matyssek R, Zimmermann R (1986) Estimation of photosynthetic rate and annual carbon gain in conifers from specific leaf weight and leaf biomass. Oecologia 70: 187-193

Oswald H (1963) Verteilung und Zuwachs der Zirbe (*Pinus cembra* L.) der subalpinen Stufe an einem zentralalpinen Standort. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 60: 437-499

Paulsen J, Weber UM, Körner Ch (2000) Tree growth near treeline. Abrupt or gradual reduction with altitude. Arctic, Antarctic, and Alpine Research 32: 14-20

Penning de Vries FTW (1975) Use of assimilates in higher plants. In: Cooper JP (ed) Photosynthesis and productivity in different environments. Cambridge University Press, London, pp 459-480

Peters J (2001) Ecophysiologia del Pino canario. Ph.D. thesis, La Laguna University

Pisek A, Kemnitzer R (1968) Der Einfluß von Frost auf die Photosynthese der Weißtanne (*Abies alba* Mill). Flora (Jena) 175: 314-326

Pisek A, Winkler E (1958) Assimilationsvermögen und Respiration der Fichte (*Picea excelsa* LINK) in verschiedenen Höhenlagen und der Zirbe (*Pinus cembra* L.) an der alpinen Waldgrenze. Planta 51: 518-543

Pisek A, Sohm H, Cartellieri E (1935) Untersuchungen über osmotischen Wert und Wassergehalt von Pflanzen und Pflanzengesellschaften der alpinen Stufe. Beiheft zum Botanischen Centralblatt 52: 634-675

Pisek A, Larcher W, Unterholzner R (1967) Kardinae Temperaturbereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verschiedener Spermatophyten. I. Temperaturminimum der Nettoassimilation, Gefrier- und Frostschadensbereiche der Blätter. Flora, Abt. B. 157: 239-543

Pisek A, Larcher W, Moser W, Pack I (1969) Kardinale Temperaturbereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verschiedener Spermatophyten. III. Temperaturabhängigkeit und optimaler Temberaturbereich der Netto-Photosynthese. Flora, Abt. B 158: 608-630

Pisek A, Larcher W, Vegis A, Napp-Zinn K (1973). The normal temperature range. In: Precht H, Christophersen J, Hensel H, Larcher W (eds) Temperature and life. Springer, Berlin, Heidelberg, New York, pp 102-194

Rada F, Azocar A, Gonzales J, Briceno B (1998) Leaf gas exchange in *Espeletia schultzii* Wedd, a giant caulescent rosette species, along an altitudinal gradient in the Venezuelan Andes. Acta Oecologia 19: 73-79

Read DJ, Haselwandter K (1981) Observations on the mycorrhizal status of some alpine plant communities. New Phytologist: 341-352

Reich PB, Koike T, Gower ST, Schoettle AW (1995) Causes and consequences of variation in conifer leaf life-span In: Smith WK, Hinckley TM (eds) Ecophysiology of coniferous forests. Academic Press, San Diego, pp 225-254

Richardson AD, Berlyn GP, Gregorie TG (2001) Spectral reflectance of *Picea rubens* (Pinaceae) and *Abies balsamifera* (Pinaceae) needles along an elevational gradient, Mt. Moosilauke, New Hampshire, USA. American Journal of Botany: 667-676

Sakai A, Larcher W (1987) Frost survival of plants. Response and adaptation to freezing stress. Ecological Studies, vol 62. Springer Berlin, Heidelberg, New York

Saxe H, Cannel MGR, Johnsen O, Ryan MG, Vourlitis G (2001) Tree and forest functioning in response to global warming. New Phytologist 149: 369-400

Schinner F (1978) Die subalpine Waldgrenze und Bedeutung der Mykotopie im Gasteiner Tal. In: Cernusca A (ed) Ökologische Analyse von Almflächen im

Gasteiner Tal. Veröffentlichungen des Österreichischen MaB-Hochgebirgsprogramms Hohe Tauern, Band 2. Universitätsverlag Wagner, Innsbruck, pp 311-314

Schulze E-D (1981) Carbon gain and wood production in trees of deciduous beech (*Fagus sylvatica*) and trees of evergreen spruce (*Picea excelsa*). Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 142: 105-123

Schulze E-D, Mooney H, Dunn EL (1967) Wintertime photosynthesis of Bristelcone pine (*Pinus aristata*) in the White Mountains of California. Ecology 48: 1044-1047

Schulze E-D, Fuchs MI, Fuchs M (1977) Spacial distribution of photosynthetic capacity and performance in a mountain spruce forest in Northern Germany. I. Biomass distribution and daily CO_2 uptake in different crown layers. Oecologia 29: 42-61

Schütz W (1968) Über die CO_2-Abgabe verholzter Achsen an der Waldgrenze. Ph.D. thesis, Innsbruck University

Schwarz W (1971) Das Photosynthesevermögen einiger Immergrüner während des Winters und seine Reaktivierungsgeschwindigkeit nach scharfen Frösten. Berichte der Deutschen Botanischen Gesellschaft 84: 585-594

Slatyer RO (1978) Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. Ex Sreng. VII. Relationships between gradients of field temperature and photosynthetic temperature optima in the Snowy Mountains area. Australian Journal of Botany 26: 111-121

Slatyer RO, Morrow PA (1977) Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. Ex Sperg. II Seasonal changes and field condition in the Snowy Mountains area of south-eastern Australia. Australian Journal of Botany 25: 1-20

Slatyer RO, Noble IR (1992) Dynamics of treelines. In: Hansen A, DiCastri F (eds) Landscape boundaries: consequences for biotic diversity and ecological flows. Ecological Studies, vol 92. Springer Berlin, Heidelberg, New York, pp 346-359

Sparks JP, Ehleringer JR (1997) Leaf carbon isotope discrimination and nitrogen content of riparian trees along an elevational gradient. Oecologia 109: 362-367

Sprugel DG, Ryan MR, Brooks JR, Vogt KA, Martin TA (1995) Respiration from the organ level to the stand. In: Smith WK, Hinckley TM (eds) Ecophysiology of coniferous forests. Academic Press, San Diego, pp 255-299

Stecher G, Schwienbacher F, Mayr S, Bauer H (1999) Effects of winter stress on photosynthesis and antioxidants of exposed and shaded needles of *Picea abies* (L.) Karst. and *Pinus cembra* L. Phyton 39: 205-212

Stevens GC, Fox JF (1991) The cause of treelines. Annual Review of Ecology and Systematics 22: 177-191

Sveinbjörnsson B (2000) North American and European treelines: external forces and internal processes controlling position. Ambio 29:388-395

Televski FW (19959 Wind-induced physiological and developmental responses in trees. In: Coutts MP, Grace J (eds) Wind and trees. University Press, Cambridge, pp 237-263

Teskey RO, Sheriff DW, Hollinger DY, Thomas RB (1995) External and internal factors regulating photosynthesis. In: Smith WK, Hinckley TM (eds) Ecophysiology of coniferous forests. Academic Press, San Diego, pp 105-140

Tranquillini W (1957) Standortklima, Wasserbilanz und CO_2-Gaswechsel junger Zirben (*Pinus cembra* L.) an der Waldgrenze. Planta 49: 612-661

Tranquillini W (1959a) Die Stoffproduktion der Zirbe (*Pinus cembra*) an der Waldgrenze während eines Jahres. I. Standortklima und CO_2-Asimilation. Planta 54: 107-129

Tranquillini W (1959b) Die Stoffproduktion der Zirbe (*Pinus cembra*) an der Waldgrenze während eines Jahres. II. Zuwachs und CO_2-Bilanz. Planta 54: 130-151

Tranquillini W (1962) Beitrag zur Kausalanalyse des Wettbewerbs ökologisch verschiedener Holzarten. Berichte der Deutschen Botanischen Gesellschaft 75: 353-364

Tranquillini W (1964) Photosynthesis and dry matter production of trees at high altitudes. In: Zimmermann MH (ed.) The formation of wood in forest trees. Academic Press, New York, pp 505-518

Tranquillini W (1969) Photosynthese und Transpiration einiger Holzarten bei verschieden starkem Wind. Centralblatt für das Gesamte Forstwesen 86: 35-48

Tranquillini W (1979) Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. Ecological Studies, vol 31. Springer Berlin, Heidelberg, New York

Tranquillini W, Machl-Ebner I (1971) Über den Einfluss von Wärme auf das Photosynthesevermögen der Zirbe (*Pinus cembra* L.) und der Alpenrose (*Rhododendron ferrugineum* L.) im Winter. Report Kevo Subarctic Research Station 8: 158-166

Tranquillini W, Schütz W (1970) Über die Rindenatmung einiger Bäume an der Waldgrenze. Centralblatt für das Gesamte Forstwesen 87: 42-60

Tranquillini W, Turner H (1961) Untersuchungen über die Pflanzentemperaturen in der subalpinen Stufe mit besonderer Berücksichtigung der Nadeltemperaturen der Zirbe. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 127-151

Turner H (1961) Jahresgang und biologische Wirkungen der Sonnen- und Himmelsstrahlung an der Waldldgrenze der Ötztaler Alpen. Wetter und Leben 13: 93-113

Turner H, Streule A (1983) Wurzelwachstum und Sprossentwicklung junger Koniferen im Klimastress der alpinen Waldgrenze, mit Berücksichtigung von Mikroklima, Photosynthese und Stoffproduktion. Wurzelökologie und ihre Nutzanwendung. Internationales Symposium Gumpenstein, 1982. Bundesanstalt Gumpenstein, pp 617-635

Turner H, Tranquillini W (1961) Die Strahlungsverhältnisse und ihr Einfluß auf die Photosynthese der Pflanzen. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 69-103

Ungerson J, Scherdin G (1968) Jahresgang der Photosynthese und Atmung unter natürlichen Bedingungenbei *Pinus sylvestris* L. an ihrer Nordgrenze in der Subarktis. Flora (Jena), Abt B. 157: 391-434

Valentini R, Matteucci G, Dolman AJ, Schulze E-D, Rebmann C, Moors EJ, Granier A, Gross P, Jensen NO, PIlegraad K, Lindroth A, Grelle A, Bernhofer Ch, Grünwald P, Aubinet M, Ceulemans R, Kowalski AS, Vesala T, Rannik U, Berbiger P, Loustau D, Gudmundsson J, Thogeirsson H, Ibrom A, Morgenstern K, Clement R, Moncrieff J, Montanini L, Minerbi S, Jarvis PG (2000) Respiration as the main determinant of carbon balance in European forests. Nature 404: 861-865

Vogt KA, Grier CC, Meier CE (1982) Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. Ecology 63: 370-380

Volgger E (1995) Zur Ozonempfindlichkeit der europäischen Lärche (*Larix decidua* Mill.) an der Waldgrenze. Diploma thesis, Innsbruck University

Waring RH, Running SW (1998) Forest Ecosystems: Analysis at multiple scales. Academic Press, San Diego

Waring RH, Schlesinger WH (1985) Forest ecology: concepts and management. Academic Press, Orlando

Wiemken V, Ineichen K (2000) Seasonal fluctuations of the levels of soluble carbohydrates in spruce needles exposed to elevated CO_2 and nitrogen fertilization and glucose as a potential mediator of acclimation to elevated CO_2. Journal of Plant Physiology 156: 746-750

Wieser G (1997) Carbon dioxide gas exchange of cembran pine (*Pinus cembra*) at the alpine timberline during winter. Tree Physiology 17: 473-477

Wieser G (2002) The role of sapwood temperature variations within *Pinus cembra* on calculated stem respiration: implications for upscaling and predicted global warming. Phyton 42: 1-11

Wieser G (2004a) Environmental control of carbon dioxide gas exchange in needles of a mature *Pinus cemra* tree at the alpine timberline during the growing season. Phyton 44: 145-153

Wieser G (2004b) Seasonal variation of soil respiration in a *Pinus cembra* forest at the upper timberline in the Central Austrian Alps. Tree Physiology 24: 475-480

Wieser G, Bahn M (2004) Seasonal and spatial variation in woody-tissue respiration in a *Pinus cembra* tree at the alpine timberline in the Central Austrian Alps. Trees 18: 576-580

Wieser G, Havranek WM (1996) Evaluation of ozone impact on mature spruce and larch in the field. Journal of Plant Physiolpogy 148: 189-194

Wieser G, Havranek WM (2001) Effects of ozone on conifers in the timberline ecotone. In: Huttunen S, Heikkilä H, Bucher J, Sundberg B, Jarvis P, Matyssek R (eds) Trends in European forest tree physiology research. Tree Physiology, vol 2. Kluwer Academic Publishers, Dordrecht, Boston, London, pp 115-125

Wieser G, Kronfuss G (1997) Der Einfluß von Dampfdruckdefizit und mildem Bodenwasserstreß auf den Gaswechsel junger Fichten (*Picea abies* [L.] Karst.). Centralblatt für das Gesamte Forstwesen 114: 173-182

Wieser G, Stöhr D (2005) Net ecosystem carbon dioxide exchange dynamics in a *Pinus cembra* forest at the upper timberline in the central Austrian Alps. Phyton 45: 233-242

Wieser G, Gigele T, Pausch H (2005) The carbon budget of an adult *Pinus cembra* tree at the alpine timberline in the Central Austrian Alps. European Journal of Forest Research 124: 1-8

Wieser G, Hecke K, Tausz M, Häberle K-H, Grams TEE, Matyssek R (2002) The role of antioxidative defense in determining ozone sensitivity of Norway spruce (*Picea abies* (L.). Karst.) across tree age: implications for the sun- and shade-crown. Phyton 42: 245-253

Woodward FI, Smith TM (1994) Predictions and measurements of the maximum photosynthetic rate, A_{max}, at the global scale. In: Schulze E-D, Caldwell MM (eds) Ecophysiology of photosynthesis. Ecological Studies, vol 100. Springer, Berlin, Heidelberg, New York, pp 492-509

Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR (1994) Evidence of reduced photosynthetic rate in old trees. Forest Science 40: 513-527

Zeller KF, Nikolov NT (2000) Quantifying simultaneous fluxes of ozone, carbon dioxide and water vapor above a subalpine forest ecosystem. Environmental Pollution 17: 1-20

Zha T, Kellomäki S, Wang KY, Rouvinen I (2004) Carbon sequestration and ecosystem respiration for 4 years in a Scots pine forest. Global Change Biology 10: 1492-1503

7 Limitation by Growth Processes

Walter Oberhuber

Institut für Botanik, Universität Innsbruck

7.1 Introduction

Growth processes involve cell division, expansion and differentiation and result in increment of dry mass, volume, length or area. Since stem growth above a certain height is one prerequosite to classify upright plants to the life-form tree (see references cited in Holtmeier 2003) and roots exert direct influences on above-ground metabolism (see below), the limitation of shoot and root growth by low temperatures during the growing season will be discussed briefly, whereby the focus will be on more recent studies.

7.2 Shoot growth at low temperatures

There is extensive evidence that at high altitudes temperature has a direct effect on formation of new tissues and tree growth (see more recent reviews by Körner 1998, 2003; Jobbagy and Jackson 2000; Grace et al. 2002). Several physiological studies found a tight coupling between warmth and meristematic activity (Hellmers et al. 1970; Juntilla 1986; Scott et al. 1987; James et al. 1994). For example, from data shown by Junttila and Nilsen (1993) and James et al. (1994) a minimum temperature between 6 and 7.5 °C for shoot growth of *Pinus sylvestris* can be deduced (cf. Fig. 7.1). Also Kanninen (1985) reports a base temperature of 6.3 °C for the response of shoot elongation of *Pinus sylvestris* to temperature. Häsler et al. (1999) found that if temperature drops below 5-7 °C shoot growth of *Larix decidua* is strongly reduced.

G. Wieser and M. Tausz (eds.), Trees at their Upper Limit, 131–143.

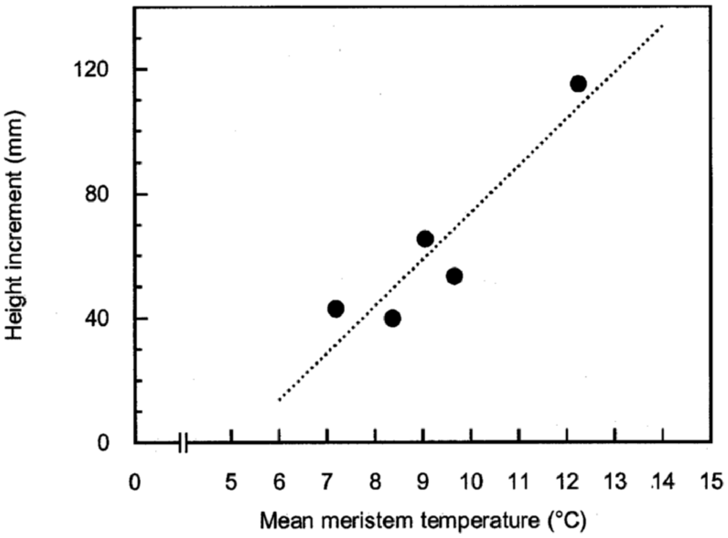

Fig. 7.1. Relationship between mean height increment of *Pinus sylvestris* and mean meristem temperature of the current growing season. (After James et al. 1994.)

Also Loris (1981) found by simultaneous measurements diameter and climatological parameters that radial growth of *Pinus cembra* ceased when temperatures fell below 5 °C. Another study on *Pinus cembra* in the Austrian Alps by Kronfuss (1994) documented also that height growth shows a strong correlation with growing season temperature.

Decreasing temperature and shortening of the growing season with altitude (see Chap. 2) causes gradually reduced shoot growth (Fig. 7.2), whereby elevation effects on tree growth are more marked in the higher elevation section especially in the subalpine zone, where the forest stand opens up and trees are isolated from each other (e.g. James et al. 1994; Paulsen et al. 2000; Li et al. 2003; and further references in Tranquillini 1979). The effect of elevation on growth of subalpine trees, however, seems to be size specific. Li et al. (2003) and Li and Yang (2004) report that elevation began to significantly affect height growth of trees growing within the subalpine areas of Tyrol (Austria) only when trees reached a certain age or exceeded a height > 0.5 m (Fig. 7.3). In the seedling stage, it was found that neither microtopography nor elevation has a strong effect on height growth. On the other hand, trees exceeding a certain height are directly coupled to atmospheric conditions, in contrast to short-stature plants, which profit from life-form driven passive solar-energy use, which facilitates canopy and soil heating (Hadley and Smith 1987; Wilson et al. 1987; Grace et al. 1989; Kronfuss and Havranek 1999; Körner 2003). Similarly, the lower sensitivity of radial growth of *Pinus sylvestris* to summer air temperature at the upper altitudinal tree-line in Scotland has been explained by the fact that the meristems are warmer in low stature plants (Grace and Norton 1990). A similar explanation has been suggested for the missing correlation between summer temperature and radial growth of *Pinus cembra* at the treeline on Mt. Patscherkofel, Austria (Oberhuber 2004).

This implies that actual meristem temperatures are more important than air temperature measured 2 m above ground. James et al. (1994) report that the temperature of the terminal meristems of *Pinus sylvestris* showed a distinct decline just above the treeline, while the air temperature did not. Generally, in tall vegetation, apical meristems experience a colder climate since meristem temperature is coupled to air temperature, whereas the meristem temperatures of short vegetation correlate strongly with net radiation (Hadley and Smith 1987; Wilson et al. 1987; Grace et al. 1989). Wilson et al. (1987) found that meristem temperatures of *krummholz*-pines (1 - 4 m height) are significantly higher than air temperature, whereby the largest difference was 10 °C and the mean difference was 4.3 °C (Fig. 7.4).

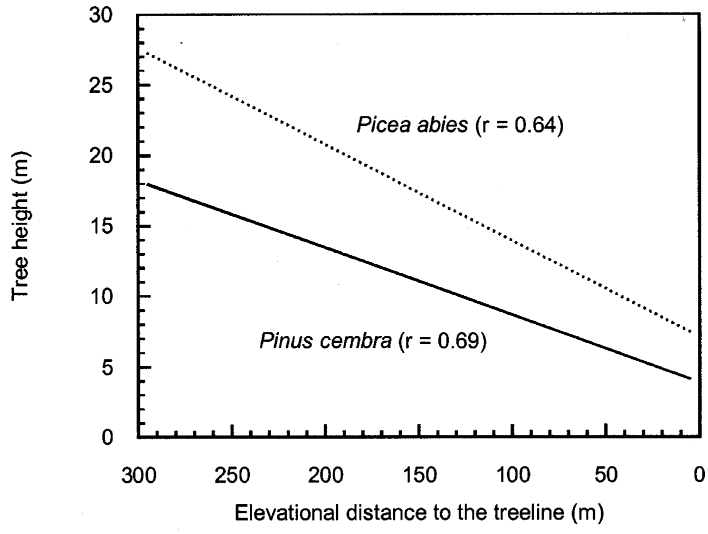

Fig. 7.2. Tree height of *Pinus cembra* and Picea *abies* across the treeline ecotone in the Swiss and Austrian Alps. (After Paulsen et al. 2000.)

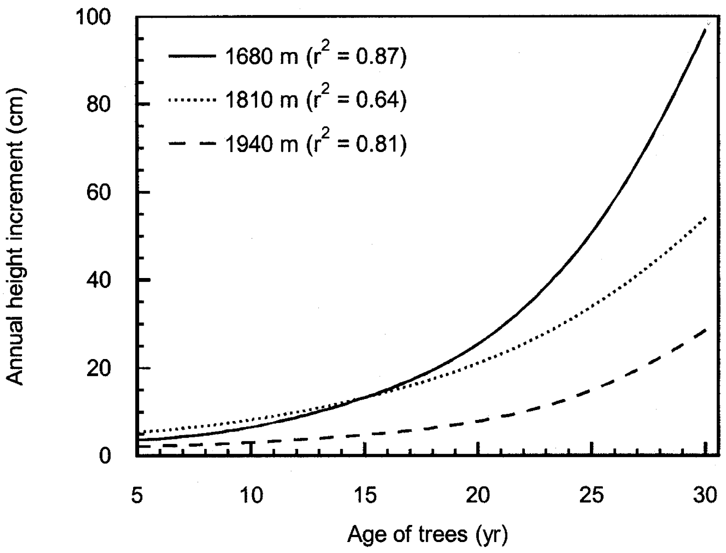

Fig. 7.3. Mean annual height increment (n = 3 plots) of *Picea abies* in relation to age at different elevations on a S-facing slope in the Central Alps, Tyrol, Austria. (After Li et al. 2003.)

The difference in the nature of this coupling appears to be entirely due to the difference in stature *per se*. Short vegetation is aerodynamically smooth, and so turbulent mixing between the air at the surface and that in the atmosphere as a whole, is correspondingly poor. Similarly, such plants in arctic, alpine and montane environments display leaf temperatures which are up to 20 °C warmer than air, displaying temperatures which fluctuate in relation to radiation and wind speed (Körner 2003). Thus, even though the dwarf vegetation occurs at a higher altitude than the tall vegetation, the meristems spend much of their day at higher temperatures than those of the trees at lower altitude.

Differences in height growth between high- and low-altitude populations have been reported by several authors (for further references see Tranquillini 1979; Holzer et al. 1979; Oleksyn et al. 1998). High altitude populations are sensitive to short days, i.e. shoot extension is commenced later and a terminal bud is formed sooner in the season compared to low altitude ecotypes. A shorter period of shoot extension and reduced growth rates of high altitude ecotypes, which were found to be primarily responsible for growth inferiority of high altitude provenances, are regarded as genetically controlled features adaptive to stressful environmental conditions at the upper treeline, e.g., occurrence of late and early frosts (cf. Tranquillini 1979).

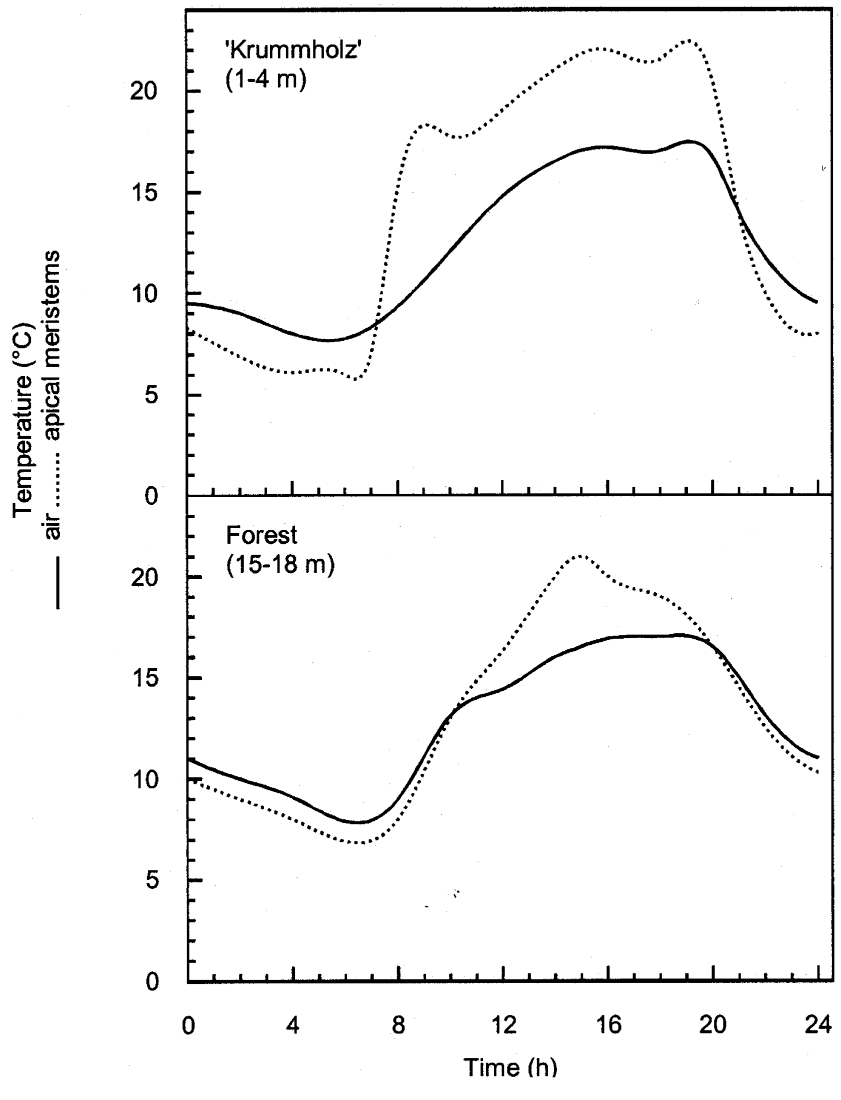

Fig. 7.4. Mean diurnal trends of temperature in June near the treeline formed by *Pinus sylvestris* in the Cairngorm Mountains, Scotland. *Pinus sylvestris* forms a natural treeline at 450 m a.s.l. and dwarf forms (*'Krummholz'*) at 600 m a.s.l. (After Wilson et al. 1987.)

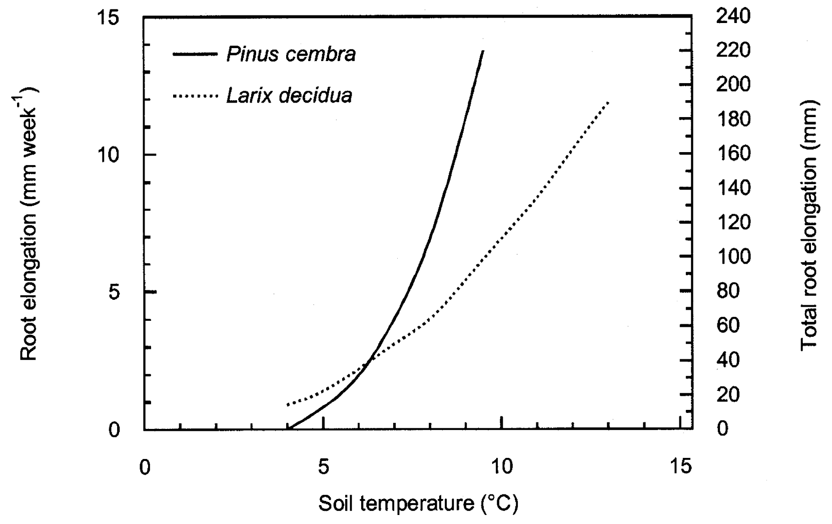

Fig. 7.5. Weekly (*Larix decidua*) and total root elongation (*Pinus cembra*) of young trees near the treeline in relation to soil temperature at 10 cm soil depth. (After Turner and Streule 1983; Häsler et al. 1999.)

Dendroecological studies reveal a close correlation between summer temperature and tree ring width and density at temperature limited alpine treeline sites (e.g. LaMarche and Fritts 1971; Eckstein and Aniol 1981; Carrer and Urbinati 2004; Oberhuber 2004). It is also reported that subalpine tree species have been facing growth increases during the 20th century, related to climate warming (Graumlich et al. 1989; Peterson and Peterson 1994; Rolland et al. 1998; Oberhuber and Kofler 2003; Bunn et al. 2005). However, the correlation of radial growth with elevation is less pronounced (see references in Tranquillini 1979; Paulsen et al. 2000; Li et al. 2003), which is related to the influence of various site factors and tree density on cambial activity (cf. Carrer and Urbinati 2001; Pfeifer et al. 2005).

7.3 Root growth at low soil temperature

At high altitudes soil temperature is regarded to be one of the most important limiting factors for root growth, including the initiation and cessation of growth (for a review see e.g. Pregitzer et al. 2000). Roots of 6 year old

Pinus cembra at the treeline in the Swiss central Alps did not grow at soil temperatures (10 cm depth) below 3 - 5 °C (Turner and Streule 1983; Fig. 7.5). There are several other studies, which also report that soil temperatures below 5 to 7 °C substantially reduce elongation rates for roots of boreal conifer species (Lyr and Hoffmann 1967; Tryon and Chapin 1983; Andersen et al. 1986; Häsler et al. 1999). That root elongation of *Larix decidua* increases faster with ambient temperature than shoot growth was reported by Häsler et al. (1999).

Soil temperature also influences above ground metabolism and growth (e.g. Havranek 1972; DeLucia 1986; Day et al. 1989; Lopushinsky and Max 1990; Domisch et al., 2001), which emphasizes the relevance of root-zone temperature for physiological processes at the treeline. Higher proportional biomass partitioning to roots of high altitude ecotypes is considered to be an adaptation to unfavourable climatic conditions, where nutrient supplies are limited (Oleksyn et al. 1998). In contrast to this, Körner and Larcher (1988) and Weih and Karlsson (1999) argue that low temperature limit plant growth in cold climates more than it does nutrient acquisition.

At the climatic treeline in the Alps mean soil temperature in 10 cm soil depth under forest trees varies from 6.4 to 7.7 °C during the growing season and reaches a maximum of *c.* 13 °C (Körner and Paulsen 2004; see Chap. 3). In contrast, alpine grasslands at 200-250 m higher elevation were mostly found to be warmer during the growing season (Körner et al. 2003), which may permit isolated trees to grow at higher elevations as they could in closed stands (Fig. 7.6A). Hence, soil temperatures found under closed forests are generally lower than those under dwarf plants or grassland above the treeline (reviewed in Körner and Paulsen 2004), since closed tree canopies prevent soil heat flux and radiative warming of their rooting zone and hence create a cold root zone (Fig. 7.6B).

Near the treeline, the microclimate is strongly related to the exposition and topography of the site (see Chap. 2). In this respect, Turner and Streule (1983) report that root growth of 6 yr old *Pinus cembra* on an E-facing slope was > 50 % higher than on an N-facing slope (cf. Häsler et al. 1999). Li et al. (2003) found that shoot growth of is also affected by microtopographical conditions, but only when the tree height was between 0.5 and 3 m. Hence, as trees exceed a certain height, tree canopies cover the ground surface and create a forest microclimate, whereby the effects of topographical conditions are successively diminished. This is supported by Körner and Paulsen (2004), who show that root-zone temperatures during the growing season below closed tree canopies do not differ between N- and S-slopes. Since Innerebner (1933) documented that air temperature 2 m above ground are similar at N and S slopes in the central Alps, apical meristems of trees > 2 m height can not profit from greater radiation warming on S-slopes during the growing season. The missing exposure effect on tree-line elevation suggested by a GIS-analysis in the Swiss Alps (Paulsen and Körner 2001) is explained by these facts.

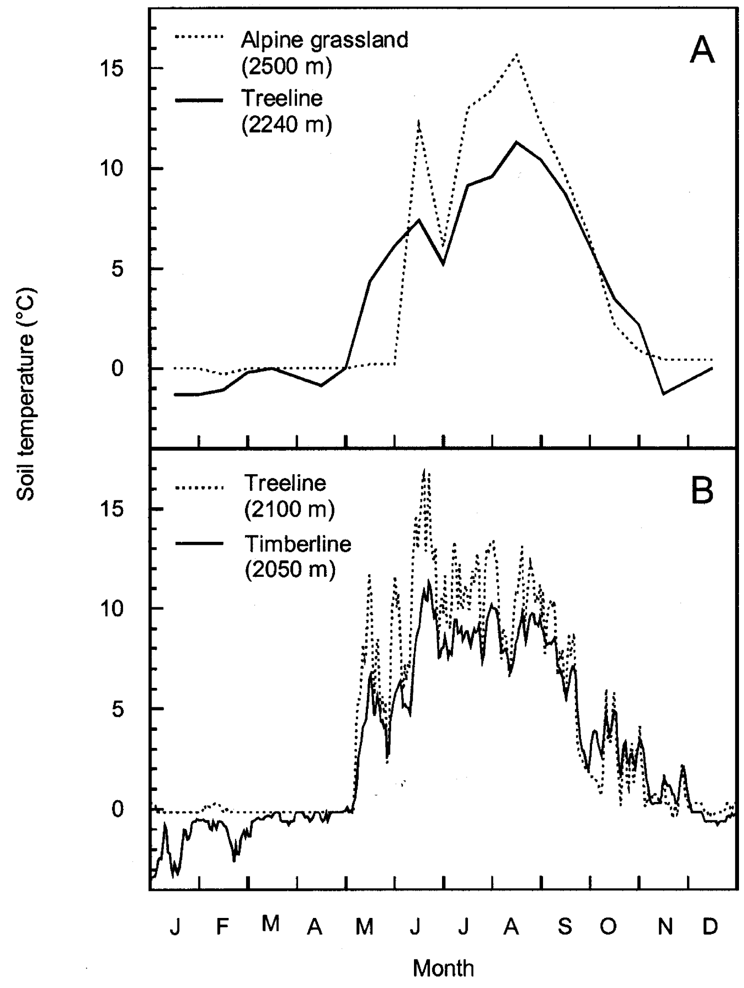

Fig. 7.6. Comparison of daily mean soil temperatures at 10 cm depth (A) under trees at the treeline in the Swiss Alps (Valais, Furka) and alpine vegetation at higher elevation (after Körner et al. 2003) and (B) at the W-facing treeline and timberline on Mt. Patscherkofel, Tyrol, Austria. (Oberhuber, previously unpublished data.)

On the other hand, the different sensitivity of radial growth of *Pinus cembra* within the treeline ecotone to climate warming and year-to-year climate variation according to slope aspect, which was reported by e.g. Villalba et al. (1994, 1997), Urbinati et al. (1997), Peterson (1998), Oberhuber and Kofler (2003), and Oberhuber (2004), seems to be related to local site specific differences in climate conditions beyond the growing season, especially more pronounced effects of winter desiccation and prolonged snow cover on tree growth at S- and N-facing slopes, respectively.

7.4 Threshold temperature for growth

The concept of a minimum temperature for tree growth (growth limitation hypothesis by Körner 1998) as an explanation of global treelines assumes that tree growth at high altitude is not limited by carbon acquisition (source inhibition), but rather by sink inhibition due to low temperature throughout the growing season. Körner and Larcher (1988) report that cell division and extension are generally more sensitive to temperature than is the rate of photosynthesis (cf. Grace et al. 2002), which is supported by several studies, where clear evidence was found that non-structural carbon charging of trees occurs as one approaches the tree limit (Hoch et al. 2002; Hoch and Körner 2003). Sveinbjörnsson (2000) however, interpreted high carbohydrate concentrations of tree line trees as an acclimation to the high risks of tissue losses.

Since environmental factors (e.g., temperature, precipitation, solar radiation) change gradually with increasing altitude and the treelines of the world occur at seasonal mean air and ground temperatures between 5.5 and 7.5 °C (Körner 1998) and 6.7 °C (Körner and Paulsen 2004), respectively, a threshold tissue temperature below which no growth processes occur is to be expected (cf. Hellmers et al. 1970; Grace 1988).

Current evidence therefore favour the view that the combined effect of apical meristems coupled to atmospheric conditions and development of cold soils under dense stands limit the life-form tree, whenever the temperatures during the growing season fall below a threshold necessary for tissue growth.

References

Andersen CP, Sucoff EI, Dixon RK (1986) Effects of root zone temperature on root initiation and elongation in red pine seedlings. Canadian Journal of Forest Research 16: 696-700

Bunn AG, Graumlich LJ, Urban DL (2005) Trends in twentieth-century tree growth at high elevations in the Sierra Nevada and White Mountains, USA. The Holocene 15: 481-488

Carrer M, Urbinati C (2001) Spatial analysis of structural and tree-ring related parameters in a timberline forest in the Italian Alps. Journal of Vegetation Science 12: 643-652

Carrer M, Urbinati C (2004) Age-dependent tree-ring growth response to climate in *Larix decidua* and *Pinus cembra*. Ecology 85: 730-740

DeLucia EH (1986) Effect of low root temperature on net photosynthesis, stomatal conductance and carbohydrate concentration in Engelmann spruce (*Picea engelmanii* Parry ex Engelm.) seedlings. Tree Physiology 2: 143-154

Domisch T, Finér L, Lehto T (2001) Effects of soil temperature on biomass and carbohydrate allocation in Scots pine (*Pinus sylvestris*) seedlings at the beginning of the growing season. Tree Physiology 21: 465-472

Eckstein D, Aniol RW (1981) Dendroclimatological reconstruction of the summer temperatures for an alpine region. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 142: 391-398

Grace J, Norton DA (1990) Climate and growth of *Pinus sylvestris* at its upper altitudinal limit in Scotland: evidence from tree growth-rings. Journal of Ecology 78: 601-610

Grace J, Allen SJ, Wilson C (1989) Climate and the meristem temperatures of plant communities near the tree-line. Oecologia 79: 198-204

Grace J, Berninger F, Nagy L (2002) Impacts of climate change on the tree line. Annals of Botany 90: 537-544

Graumlich L, Brubaker LB, Grier CC (1989) Long-term growth trends in forest net primary productivity: Cascade Mountains, Washington. Ecology 70: 405-410

Hadley JL, Smith WK (1987) Influence of krummholz mat microclimate on needle physiology and survival. Oecologia 73: 82-90

Häsler R, Streule A, Turner H (1999) Shoot and root growth of young *Larix decidua* in contrasting microenvironments near the alpine timberline. Phyton 39: 47-52

Havranek W (1972) Über die Bedeutung der Bodentemperatur für die Photosynthese und Transpiration junger Forstpflanzen und für die Stoffproduktion an der Waldgrenze. Angewandte Botanik 46: 101-116

Hellmers H, Genthe MK, Ronco F (1970) Temperature affects growth and development of Engelmann spruce. Forest Science 16: 447-452

Hoch G, Körner Ch (2003) The carbon charging of pines at the climatic treeline: a global comparison. Oecologia 135: 10-21

Hoch G, Popp M, Körner Ch (2002) Altitudinal increase of mobile carbon pools in *Pinus cembra* suggests sink limitation of growth at the Swiss treeline. Oikos 98 361-374

Holtmeier F-K (2003) Mountain timberlines. Ecology, patchiness, and dynamics. Advances in Global Change Research, vol 14. Kluwer Academic Publishers, Dordrecht, Boston, London

Holzer K, Oberarzbacher P, Unterholzner L, Tranquillini W (1979) Über das Wachstum von Klonen der Fichte in Klimakammern [*Picea abies* (L.) Karsten]. Centralblatt für das Gesamte Forstwesen 96: 74-86

Innerebner F (1933) Über den Einfluß der Exposition auf die Temperaturverhältnisse im Gebirge. Meteorologische Zeitschrift 50: 337-346

James JC, Grace J, Hoad SP (1994) Growth and photosynthesis of *Pinus sylvestris* at its altitudinal limit in Scotland. Journal of Ecology 82: 297-306

Jobbagy EG, Jackson RB (2000) Global controls of forest line elevation in the northern and southern hemispheres. Global Ecology and Biogeography 9: 253-268

Juntilla O (1986) Effects of temperature on shoot growth in northern provenances of *Pinus sylvestris* L. Tree Physiology 1: 185-192

Juntilla O, Nilsen J (1993) Growth and development of northern forest trees as affected by temperature and light. In: Alden J, Mastrantonio JL, Odum S (eds) Forest development in cold climates. Plenum Press, New York, pp 43-57

Kanninen M (1985) Shoot elongation in Scots Pine: Diurnal variations and response to temperature. Journal of Experimental Botany 36: 1760-1770

Kirdyanov A, Hughes M, Vaganov E, Schweingruber F, Silkin P (2003) The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic. Trees 17: 61-69

Körner Ch (1998) A re-assessment of high elevation treeline positions and their explanation. Oecologia 115: 445-459

Körner Ch (2003) Alpine plant life: functional plant ecology of high mountain ecosystems, 2nd edn. Springer, Berlin

Körner Ch, Larcher W (1988). Plant life in cold climates. In: Long SP, Woodward FI (eds) Plants and temperature. Symposia of the Society for Experimental Biology, vol 42. Cambridge, pp 25-57

Körner Ch, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. Journal of Biogeography 31: 713-732

Körner Ch, Paulsen J, Pelaez-Riedl S (2003). A bioclimatic characterisation of Europe's alpine areas. In: Nagy L, Grabherr G, Körner Ch, Thompson DBA (eds) Alpine biodiversity in Europe. Ecological Studies, vol 167. Springer-Verlag Berlin, Heidelberg, pp 13-28

Kronfuss H (1994) Der Einfluß der Lufttemperatur auf das Höhenwachstum der Zirbe. Centralblatt für das Gesamte Forstwesen 111: 165-181

Kronfuss H, Havranek WM (1999) Effects of elevation and wind on the growth of *Pinus cembra* L. in a subalpine afforestation. Phyton 39: 99-106

LaMarche VC, Fritts HC (1971) Tree rings, glacial advance, and climate in the Alps. Zeitschrift Gletscherkunde Glazialgeologie 7: 125-131

Li MH, Yang J (2004) Effects of microsite on growth of *Pinus cembra* in the subalpine zone of the Austrian Alps. Annals of Forest Science 61: 319-325

Li MH, Yang J, Kräuchi N (2003) Growth response of *Picea abies* and *Larix decidua* to elevation in subalpine areas of Tyrol, Austria. Canadian Journal of Forest Research 33: 653-662

Lopushinsky W, Max TA (1990) Effect of soil temperature on root and shoot growth and on budburst timing in conifer seedling transplants. New Forests 4: 107-124

Loris K (1981) Dickenwachstum von Zirbe, Fichte und Lärche an der alpinen Waldgrenze/Patscherkofel. Mitteilungen der Forstlichen Bundesversuchsansalt Wien 142: 417-441

Lyr H (1996) Effect of the root temperature on growth parameters of various European tree species. Annales des Sciences Forestières 53: 317-323

Lyr H, Hoffmann G (1967) Growth rates and growth periodicity of tree roots. International Review of Forestry Research 2: 181-236

Oberhuber W (2004) Influence of climate on radial growth of *Pinus cembra* within the alpine timberline ecotone. Tree Physiology 24: 291-301

Oberhuber W, Kofler W (2003) Effects of climate and slope aspect on radial growth of cembran pine (*Pinus cembra* L.) at the alpine timberline ecotone on Mt. Patscherkofel (Tyrol, Austria). Austrian Journal of Forest Science 120: 39-50

Oleksyn J, Modrzynski J, Tjoelker MG, Zytkowiak R, Reich PB, Karolewski P (1998) Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. Functional Ecology 12: 573-590

Ott E (1978) Über die Abhängigkeit des Radialzuwachses und der Oberhöhen bei Fichte und Lärche von der Meereshöhe und Exposition im Lötschental. Schweizerische Zeitschrift für Forstwesen 129: 169-193

Paulsen J, Körner Ch (2001) GIS-analysis of tree-line elevation in the Swiss Alps suggests no exposure effect. Journal of Vegetation Science 12: 817-824

Paulsen J, Weber UM, Körner Ch (2000) Tree growth near treeline: abrupt or gradual reduction with altitude? Arctic, Antarctic, and Alpine Research 32: 14-20

Peterson DL (1998) Climate, limiting factors and environmental change in high-altitude forests of Western North America. In: Beniston M, Innes JL (eds) The impacts of climate variability on forests. Lecture Notes in Earth Science, vol 74. Springer-Verlag, Berlin, pp 191-208

Peterson DW, Peterson DL (1994) Effects of climate on radial growth of subalpine conifers in the North Cascade Mountains. Canadian Journal of Forest Research 24: 1921-1932

Pfeifer K, Kofler W, Oberhuber W (2005) Climate related causes of distinct radial growth reductions in *Pinus cembra* during the last 200 yr. Vegetation History and Archaeobotany 14: 211-220

Pregitzer KS, King JS, Burton AJ, Brown SE (2000) Responses of tree fine roots to temperature. New Phytologist 147: 105-115

Rolland C, Petitcolas V, Michalet R (1998) Changes in radial tree growth for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline since 1750. Trees 13: 40-53

Scott PA, Bentley CV, Fayle DCF, Hansell RIC (1987) Crown forms and shoot elongation of white spruce at the treeline, Churchill, Manitoba, Canada. Arctic and Alpine Research 19: 175-186

Sveinbjörnsson B (2000) North American and European treelines: external forces and internal processes controlling position. Ambio 29: 388-395

Tranquillini W (1979) Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. Ecological Studies, vol 31. Springer, Berlin, Heidelberg, New York

Tryon PR, Chapin FSIII (1983) Temperature control over root growth and root biomass in taiga forest trees. Canadian Journal of Forest Research 13: 827-833

Turner H, Streule A (1983) Wurzelwachstum und Sprossentwicklung junger Koniferen im Klimastress der alpinen Waldgrenze, mit Berücksichtigung von Mikroklima, Photosynthese und Stoffproduktion. Wurzelökologie und ihre Nutzanwendung. Internationales Symposium Gumpenstein, 1982. Bundesanstalt Gumpenstein, pp 617-635

Urbinati C, Carrer M, Sudiro S (1997) Dendroclimatic response variability of *Pinus cembra* L. in upper timberline forests of Italian Eastern Alps. Dendrochronologia 15: 101-117

Villalba R, Veblen TT, Ogden J (1994) Climatic influences on the growth of subalpine trees in the Colorado Front Range. Ecology 75: 1450-1462

Villalba R, Boninsegna JA, Veblen TT, Schmelter A, Rubulis S (1997) Recent trends in tree-ring records from high elevation sites in the Andes of northern Patagonia. Climatic Change 36: 425-454

Weih M, Karlsson PS (1999) Growth response of altitudinal ecotypes of mountain birch to temperature and fertilisation. Oecologia 119: 16-23

Wilson C, Grace J, Allen S, Slack F (1987) Temperature and stature: a study of temperatures in montane vegetation. Functional Ecology 1: 405-413

8 Limits in Water Relations

Stefan Mayr

Institut für Botanik, Universität Innsbruck

8.1 Introduction

Plant water relations at the timberline reflect the special climatic conditions of this alpine ecotone. While many species are protected from climatic extremes by their microclimates, the life form "tree" with its upright habitus is closely coupled to the atmospheric environment. The following chapter deals with the components of tree water relations and focus on differences between summer and winter season. After a brief description of relevant climatic aspects, the transpiration process is discussed first because it is the driving force in the soil-plant-atmosphere continuum. Next, water transport and water uptake are dealt with and lead to the final section on water balance of alpine trees at the timberline.

8.2 Precipitation, soil moisture and evaporation

In many mountains of the world, an elevational increase in annual precipitation is observed (e.g. Körner 1999). Timberline regions in the European Alps also show high precipitation sums, although dry conditions can occur in the lee of high mountains (e.g. Tranquillini 1979). Evaporative forces decrease with altitude due to lower air temperatures, but this is often compensated by overheating effects caused by the intense radiation. Therefore, daily evapotranspiration values within the vegetation period are similar to that of low altitude while the annual sum of evapotranspiration at the timberline is reduced.

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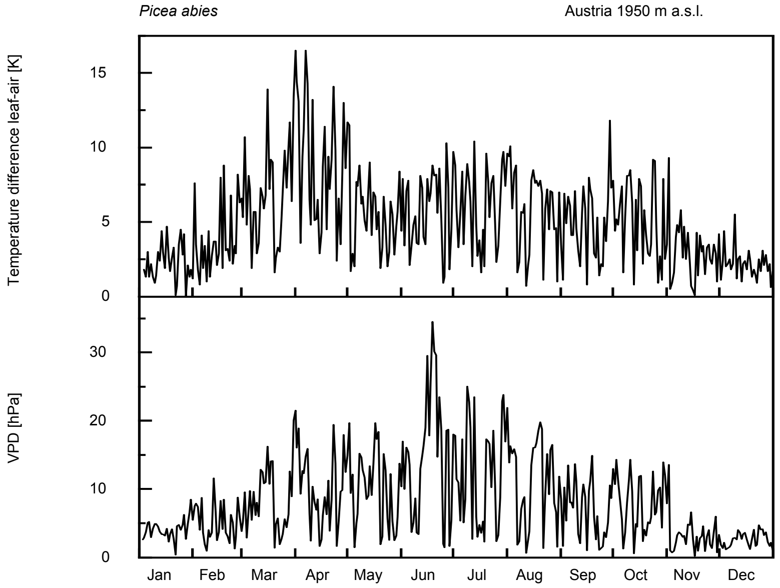

Fig. 8.1. Midday differences (12:00) in temperature between Norway spruce needles and air and corresponding water vapour pressure deficit (VPD) at Praxmar, Tyrol in 2002.

High precipitation and moderate evaporative forces lead to soil water contents, which are normally sufficient for plant water supply during the summer season. Conditions may vary on a small scale dependent on soil structure, rainfall distribution, and vegetation cover. For example, in the Italian Dolomites Anfodillo et al. (1998) showed tree predawn water potentials of -1 MPa, which indicate low soil potentials. However, Körner (1999) analysed various mountains all over the world and concluded that "soil moisture is unlikely to exert major direct physiological limitations on alpine plant life".

In winter, conditions for plants and especially for trees are less favorable. On the one hand, overheating strongly influences evaporation as shown in Fig. 8.1. High radiation amplified by reflection from the snow (Turner 1961) leads to an increased temperature of objects protruding from the snow cover. Overheating of needles above air temperatures is highest in late winter and can reach more than 15 K. Thus, the maximum evaporative force in late winter is similar to summer values (except an extraordinary period in June). On the other hand, frozen soils totally block the access to soil water resources. The duration and depth of freezing periods in the soil mainly depend on the snow cover as demonstrated by Aulitzky (1961) or Platter (1976). Early snow fall and a permanent snow cover during winter can prevent soils to reach sub-zero temperatures. In contrast, wind exposed sites were found to freeze permanently and down to a depth of 1 m. Freezing and thawing events in soil and roots do not only determine how often and how long plant water uptake is blocked but also influence water movements between tree parts embedded in the soil and tissues above the ground.

8.3 Transpiration

Transpiration is driven by the humidity gradient between the leaf and the atmosphere and thereby strongly influenced by temperature (Fig. 8.1). At the alpine timberline, an increase of transpiration by overheating effects is especially relevant during the winter season (see Chaps. 2.4 and 8.2). Therefore, the transpirational control of trees has to be optimised for minimal water losses in winter and a maximum photosynthetic yield during the short vegetation period.

Leaf conductance for water vapour measured in the summer season indicates that trees at the timberline normally do not have to restrict transpiration. Figure 8.2 demonstrates that *Larix decidua* exhibits an even higher stomatal conductance when compared to specimen at low altitude. Anfodillo et al. (1998) suggested that the deciduous strategy of larch requires an increased leaf conductance to compensate for the short vegetation period. An osmotic adjustment enables *Larix* to maintain this high stomatal conductance during summer (Badalotti et al. 2000). Körner and Cochrane (1985) also found mean and maximum leaf conductances in *Eucalyptus pauciflora* to increase with altitude. There are also species operating with a water-saving strategy like *Pinus cembra* (Anfodillo et al. 1998). However, a plot of relative conductance (Fig. 8.2) reveals that trees at the timberline and at low altitude show a similar stomatal regulation upon increasing vapour pressure deficits. Also Benecke et al. (1981) found similar correlations of stomatal conductance and the leaf-air humidity gradient at different altitudes in *Larix decidua*. The stomatal control was also closely related to light intensities. These findings indicate that trees at the alpine timberline can risk an over all higher leaf conductance although the stomatal regulation at this higher level does not differ from trees at low altitudes. There are probably exceptions to this general trend, as e.g. in several Himalayan *Picea* species an elevational decrease in foliage area per stem cross sectional area and per root mass was observed (Li et al. 2004). This may be an adaptation to increasing drought stress.

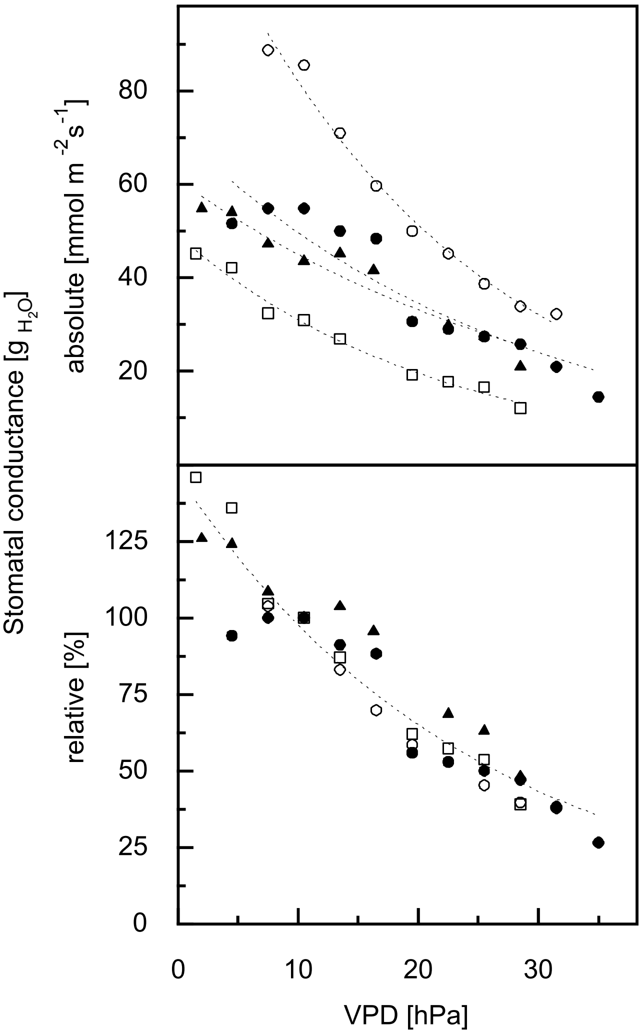

Fig. 8.2. Absolute and relative stomatal conductance at 1950 m (open symbols) or 1000 m (closed symbols) of Larix decidua (circle), Picea abies (triangle) and Pinus cembra (square) related to the vapour pressure deficit (VPD) between leaf and air. For the calculation of relative conductance, the absolute stomatal conductance at 10 hPa VPD was set to 100 %. (Modified after Wieser 2002.)

In winter, restrictions in water supply force trees to reduce transpirational water losses. Stomatal closure occurs in autumn (e.g. Christersson 1972; Havranek 1972; Larcher 1972; Goldstein et al. 1985) when soil and air temperatures decrease. Smith et al. (1984) observed a correlation between minimum night air temperatures and leaf conductance of several species in the Rocky Mountains. Bauer et al. (1994) demonstrated that in frost hardened conifers such as *Picea abies*, *Pinus cembra* and *Pinus sylvestris* the reduced stomatal conductance is the response to the reduced photosynthetic capacity. Abscisic acid, which is known to be an important signal for stomatal closure, was found to be 1.5-fold higher in winter when compared to the vegetation period (*Pinus cembra*; Christmann et al. 1999).

At the European Alps timberline, trees show closed stomata usually from November to April (Michaelis 1934a; Tranquillini 1976, 1979). However, conifer species still exhibit some transpiration over the cuticula and probably over incompletely closed stomata during the winter months. Deciduous trees avoid these water losses by shedding of their leaves. Minimum needle conductance of some evergreen species is relatively moderate (*Pinus cembra*: 3 to 10 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; Wieser 2000; Mayr et al. 2003d) while other trees exhibit extraordinary high values, like *Picea abies* (40 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; Mayr et al. 2003d; see also Baig and Tranquillini 1976; Anfodillo et al. 2002). Michaelis (1934ab) hypothesized that this phenomenon is related to the short vegetation period at the timberline, which leads to an insufficient maturation of needles and their cuticular layers (Günthardt and Wanner 1982; Tranquillini and Platter 1983). It was shown that the thickness of the cuticle of *Picea abies* and *Pinus cembra* decreases with altitude (Baig and Tranquillini 1976), and that cuticular transpiration rates of several species increase (Baig et al. 1974; Sowell et al. 1982; Tranquillini 1974; Platter 1976). Tranquillini (1976) found needles of *Picea abies* growing at upper sites of the treeline to have an even 7-fold higher cuticular transpiration than needles of the valley. Thereby, current year needles exhibit a lower cuticular resistance than older needles (Baig et al. 1974). Additionally, strong winds may damage the surface of needles by ice-blast and further decrease the cuticular resistance (e.g. Holzer 1959; Hadley and Smith 1983, 1986, 1989; Van Gradingen et al. 1991). Only shrub-like woody species like *Pinus mugo* (Mayr et al. 2003b) and young trees (Hadley and Smith 1986; Boyce and Lucero 1999; also see Fig. 8.4) are protected from transpirational water losses by the snow cover.

8.4 Water Transport

Trees evolved complex water transport systems to span the distance between the mesophyll and the roots. These transport systems are characterized by their hydraulic efficiency and safety, whereby a trade-off between these aspects is often observed (e.g. Tyree et al. 1994). The lower the resistance in the xylem the higher is its hydraulic efficiency, but a low resistance often corresponds to an increased risk of embolism induced by drought or freeze-thaw events (e.g. Zimmermann 1983; Tyree et al. 1994; Hacke and Sperry 2001).

The water transport system of trees growing at the timberline is exposed to several stress factors. Low temperatures limit the growth of wood and therefore influence its structure and properties. For instance, Boyce and Saunders (2000) demonstrated for *Picea engelmannii* and *Abies lasiocarpa*, that low summer temperatures inhibit xylem formation and affect the water transport in consecutive months. The xylem of conifers at high altitudes is usually very dense due to narrow tracheids with thick cell walls and exhibits a high lignin content as shown for *Picea abies* along altitudinal transects (Gindl et. al 2001; Mayr et al. 2002). Low temperatures as well as rapid and frequent temperature changes may also directly affect xylem structures although visible damage such as frost cracks are rare. Furthermore, it has to be considered that the tree xylem has not only a hydraulic but also a mechanical function. High wind speeds or heavy snow loads may force a mechanical optimization of wood, e.g. by formation of compression wood. Compression wood was demonstrated to have a limited hydraulic efficiency and safety (Mayr and Cochard 2003).

The specific hydraulic conductivity (k_s, related to the xylem cross sectional area; e.g. Tyree et al. 1994) of trees at the timberline is similar or lower than at low altitude. Subalpine *Pinus* species exhibit k_s (*Pinus cembra* 4.1 10^{-4}, *Pinus mugo* 2.9 $10^{-4} \cdot m^{2} \cdot s^{-1} \cdot MPa^{-1}$) comparable to those of other pine species (see Martinez-Vilalta et al. 2004). In contrast, conductivities in twigs of *Picea abies* decreased from 8.7 10^{-4} $m^{2} \cdot s^{-1} \cdot MPa^{-1}$at 800 m to 4.8 $10^{-4} m^{2} \cdot s^{-1} \cdot MPa^{-1}$ at 2100 m (Mayr et al. 2003a, c, d, unpublished data).

The hydraulic safety of (sub)alpine conifer species was found to be relatively high but within the range of low altitude species. Upon dehydration, *Pinus cembra* twigs reached 50 % loss of conductivity at a water potential of -3.5 MPa (Mayr et al. 2003d) which is similar to many other pine species (see Martinez-Vilalta et al. 2004). In contrast, the needle xylem of alpine *Pinus* species (*Pinus cembra, Pinus mugo*) was found to be significantly less vulnerable against xylem deformation as well as embolism when compared with *Pinus nigra* and *Pinus sylvestris* (Cochard et al. 2004). Although conifers are known to be very resistant to freeze-thaw induced embolism (e.g. Sperry and Sullivan 1992;, Sperry et al. 1994), the high number of freezing events at the timberline can cause excessive conductivity losses (Mayr et al. 2003a, d). *Pinus cembra* thereby was found to be more resistant than *Picea abies*. Zweifel and Häsler (2000) demonstrated that large water shifts between the bark and the xylem occur in

Picea abies upon freeze-thaw events. Unfortunately, no data on vulnerabilities of alpine angiosperms are available.

Vulnerability properties of alpine trees are probably sufficient to avoid dysfunction of the water transport system during summer (Fig. 8.3). Relatively low transpiration rates and high soil water contents reduce tensions in the xylem. During the growing season, Anfodillo et al. (1998) found minimum water potentials of -1.2 MPa in *Picea abies*, -1.5 MPa in *Pinus cembra*, and -1.9 MPa in *Larix decidua*. In all species, vulnerability thresholds for embolism are lower. However, it cannot be excluded that at extreme sites (e.g. wind exposed stands) or during prolonged drought periods, water potentials might reach these vulnerability thresholds.

In winter, frost-drought as well as frequent freeze-thaw events are known to cause xylem dysfunction in some species. In *Picea abies*, up to 100% embolism was observed in sun exposed twigs (Fig. 8.3). In these twigs, water potentials can reach less than -4 MPa and the xylem can be exposed to more than 100 freezing cycles during the winter season (Groß et al. 1991; Mayr et al. 2002, 2003a, d). Winter embolism in conifers was also reported e.g. by Sperry and Sullivan (1992), Sperry et al. (1994), and Sparks et al. (2001). In *Larix lyallii* and *Pinus albicaulis* growing at the upper timberline, conductivity losses of up to 30% were correlated with freeze-thaw events, warm weather periods and low stem water contents (Sparks and Black 1998). Shrubs (Mayr et al. 2003b) and young trees are protected by the snow cover from drought (Hadley and Smith 1983) and frost cycles and therefore from embolism (Fig. 8.4).

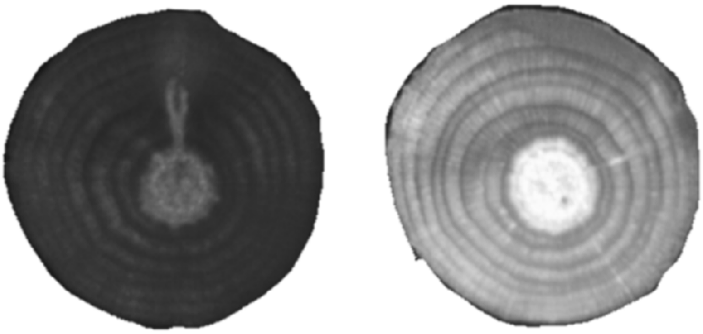

Fig. 8.3. Norway spruce twigs harvested in summer (left) and winter (right) at 2050 m and perfused with a Phloxine B solution. Light areas on the right cross section indicate non-conductive areas caused by winter-embolism.

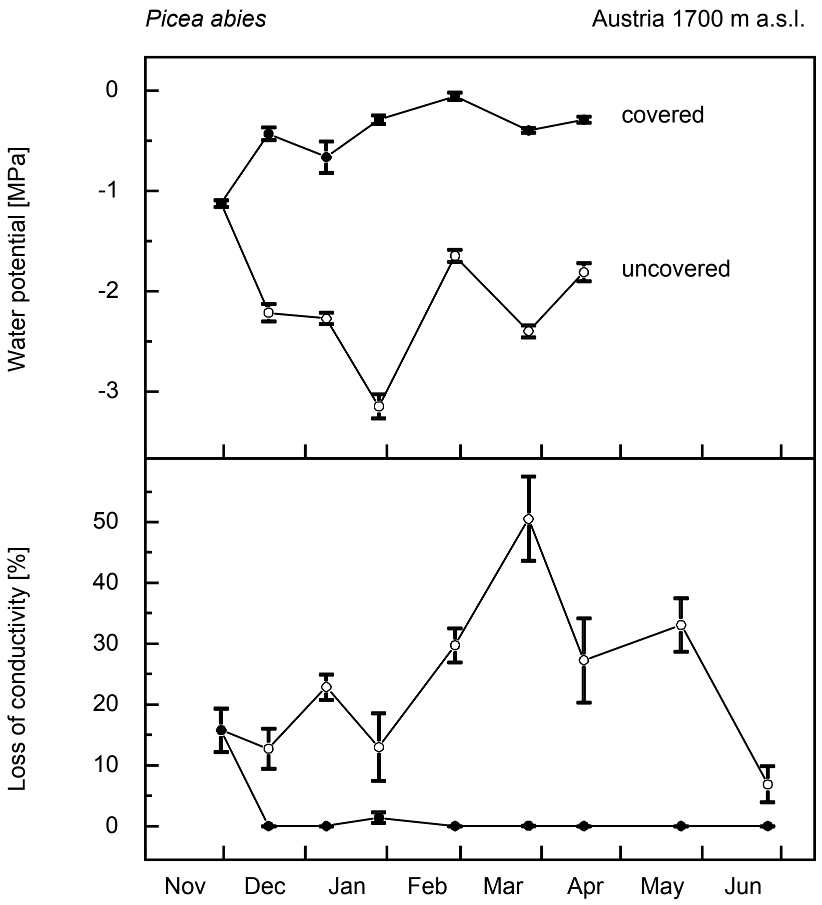

Fig. 8.4. Water potential and loss of conductivity of 5-yr old Norway spruce trees below the snow cover or artificially uncovered from snow during winter 2001/2002 at Praxmar, Tyrol. All trees were snow-free until December, embolised trees showed recovery between April and June. Mean ±SE .

(Sub)alpine species show several adaptations to avoid embolism (Mayr et al. 2003a, b, c, d), whereby *Pinus cembra* seems to be especially well protected. There are indications that some tree species have repair mechanisms to reactivate embolised sections of their water transport system (Sperry and Sullivan 1992; Sperry et al. 1994; Mayr et al 2003d; also see Fig. 8. 4). The mechanism of this process, which starts even before the soil thaws, is unknown. Katz et al. (1989) and Sparks et al. (2001) suggested water uptake by branches or leaves.

8.5 Water uptake

At the timberline, root systems of trees have to maintain water uptake despite limiting conditions for growth and function. Roots of (sub)alpine species are able to penetrate rocky undergrounds or even to grow around rocks to reach the soil. *Pinus cembra* ("stone pine"!) seeds are often hidden and forgot by jays (*Nucifraga caryocatactes*) at the top of rocks (Mattes 1982). The main roots of trees developed from these seeds are able to span distances of several meters to enable access to soil water resources. Other alpine species are known to evolve especialyl deep and efficient root systems like *Larix decidua* (Anfodillo et al. 1998). Nevertheless, low soil temperatures totally restrict root growth from early autumn to late spring and reduce growth rates in summer (e.g. Tranquillini 1973, 1979; Häsler et al. 1999). Körner (1998) suggested that trees at the timberline are sink-limited due to reduced soil temperatures caused by shading effects of the tree itself (also see Körner 1999).

Low soil temperatures at the alpine timberline do not only limit the growth of roots but also their function in water uptake. Although soil water content normally is sufficient for plant water uptake during summer (see 3.2.3. and 8.1.) low temperatures can impair water uptake. In *Picea glauca* growing at the treeline in Alaska, a reduction in water uptake was found already at a soil temperature of 9 °C (Goldstein et al. 1985).

Low soil temperatures restrict the water availability for plants also during the whole winter season. Even when the soil does not freeze (because of an insolating snow cover; see also Chap. 8.1), water uptake is limited by low soil temperatures until spring. Tranquillini (1979) estimated that water uptake is usually blocked from December to April at stands with little or no snow cover. At Praxmar, Tyrol water uptake was prevented by the frozen soil, frozen roots and the frozen stem base for a similar duration (Mayr et al. 2003d) although a permanent snow cover was present. The reactivation of water uptake in spring is not possible until the soil and the stem base are thawed. Sap flow measurements (Fig. 8.5) show that this reactivation can occur very rapidly when the soil stays frozen until late April. In contrast, sap flow rates increased slowly and stepwise when the soil and the stem base thawed early in spring.

Freezing and thawing events which can occur in upper soil layers especially in spring and autumn may cause the formation of embolism in the root xylem (also see 8.4.). Fine roots are known to be especially vulnerable to embolism and to act as "fuses" for the water transport system (Sperry and Ikeda 1997; Kavanagh et al. 1999; Hacke et al. 2000).

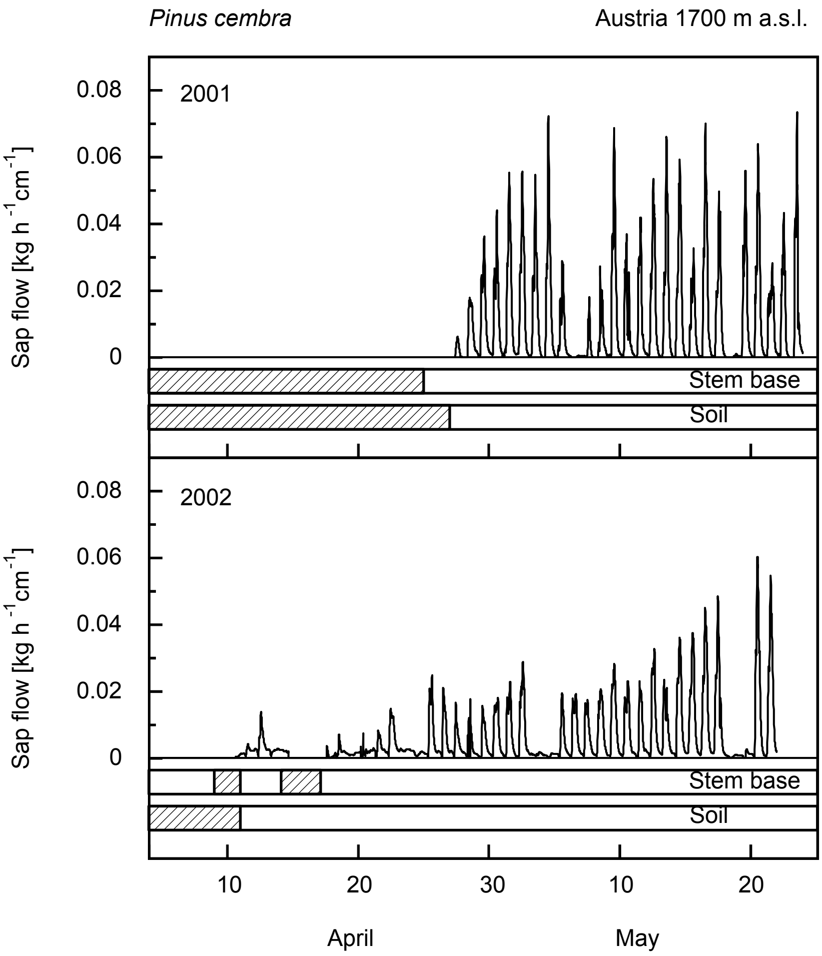

Fig. 8.5. Sap flow in the stem of a stone pine in spring 2001 and 2002. Hatched bars indicate periods of sub-zero temperatures in the xylem of the stem base and in the soil (depth 5cm). (Modified after Mayr et al. 2003d and unpublished data.)

8.6 Water balance

At the alpine timberline, plant water relations in summer and winter differ remarkably. Previous chapters showed that enormous differences can be found in all sections of the soil-plant-atmosphere continuum. Figure 8.6 demonstrates a typical annual course with moderate water potentials during summer and much lower values in the cold season. In spring and autumn, a transition between these contrary situations takes place.

Sufficient soil water contents, moderate temperatures and evaporative forces usually enable balanced tree water relations during summer (Tranquillini 1979). Within trees, dependent on their hydraulic architecture (Zimmermann 1978; Kuuluvainen et al. 1996; Mayr et al. 2003c), water potential gradients normally occur during daytime while potentials equalize over night. Only at exposed sites or during prolonged drought periods, some tree species might be exposed to drought stress. For instance, in *Larix decidua* low predawn water potentials were observed while *Picea abies* and *Pinus cembra* at the same site reached only slightly negative potentials (Anfodillo et al. 1998; Badalotti et al. 2000). However, even minimum potentials were not critical for trees as e.g. they did not reach vulnerability thresholds for xylem dysfunction. For adult *Pinus canariensis* growing at the timberline at Tenerife, Giger and Leuschner (2004) reported a minimum needle water potential of -2.5 MPa during the dry season, which is also not limiting for the trees. Nevertheless, the summer season may have long-term effects on tree water relations as temperatures influence the cuticula formation and therefore the transpiration rates of consecutive periods (Baig et al. 1974).

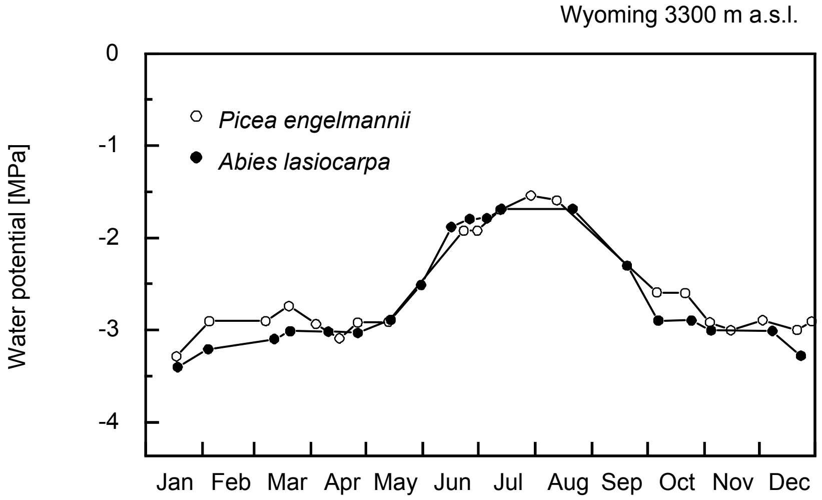

Fig. 8.6. Seasonal course of leaf water potentials in two conifers growing at the timberline of the Medicine Bow Mountains, Wyoming. (Modified after Lindsay 1971.)

In autumn, trees undergo a hardening phase and prepare for a period of strained water relations. A reduction in stomatal transpiration has to occur in time, to fill up water reservoirs and before falling temperatures limit water uptake. Otherwise, trees would enter the winter period already with low water potentials. Large trees are probably better prepared for the winter season than small trees because they can store larger amounts of water in their axes xylem (Larcher 1963). Boyce and Lucero (1999) demonstrated for *Picea engelmannii* that also roots may function as important water reservoirs during winter unless the soil is frozen.

Winter causes extreme demands on water relations of trees protruding from the snow cover. Blocked water uptake on the one hand and transpirational water losses due to overheating effects on the other, continuously impair their water status. With respect to tree water relations, a winter is strong when water uptake breaks down early in autumn, the soil stays frozen until late spring, and many cold but sunny days occur. Even deciduous species can dehydrate extremely. In the Rocky Mountains, Richards and Bliss (1986) observed water potentials down to -5.3 MPa in *Larix lyallii*. In the European Central Alps, desiccation damage was also observed regularly in *Larix decidua* (Tranquillini and Platter 1983). Only small trees covered by snow during long periods are well protected from dehydration (e.g. Lindsay 1971; Hadley and Smith 1983; Boyce and Lucero 1999; Fig. 8.5).

The most critical situation in tall trees can be found in late winter, when water potentials are already very low. In *Picea abies*, water potentials can fall below -4 MPa (Mayr et al. 2002). At this time, evaporative forces are high and lead to a further dehydration of the plant. In addition, low water potentials and accumulated numbers of freeze-thaw events cause dysfunction of the water transport system. In contrast to summer relations, stress intensities are not homogeneous within trees as for example twigs below the snow are protected from water losses and freeze-thaw events. Furthermore, frozen xylem sections cause a complex and dynamic pattern of hydraulic sub-systems within trees. During sunny periods, shaded twigs can exhibit even lower water potentials than sun exposed twigs. This occurs, when only the latter thaw at their base and get access to stem water resources (Mayr et al. 2003d). Trees can loose more than 50 % of their water reserves during the winter months (Tranquillini 1957). This period of water stress ends abruptly, when trees regain their access to soil water resources. In spring, water potentials increase and water reservoirs are filled up again.

The seasonal course of water potentials (Fig. 8.6) indicates that limitations for tree life at the timberline most probably occur in the winter season. Tranquillini (1979) published impressive photos of conifers damaged during winter and stated that "there can be no doubt that damage to shoots and needles above the winter snow cover is caused by frost desiccation" (also see Larcher 1972, 1985; Tranquillini 1979, 1980, 1982; Wardle 1981; Hadley and Smith 1986). According to the theory of Michaelis (Michaelis 1934a, b; also see Chap. 8.3.), this drought damage can often be found at the upper border of the timberline, where insufficient cuticle maturation causes high transpirational water losses (Tranquillini and Platter 1983; Hadley and Smith 1990; Mayr et al. 2002). The extent of damage depends on the intensity of climatic stress factors during winter and on species-specific transpiration rates and vulnerability thresholds. Körner (1999) gives an overview of species not affected by drought stress.

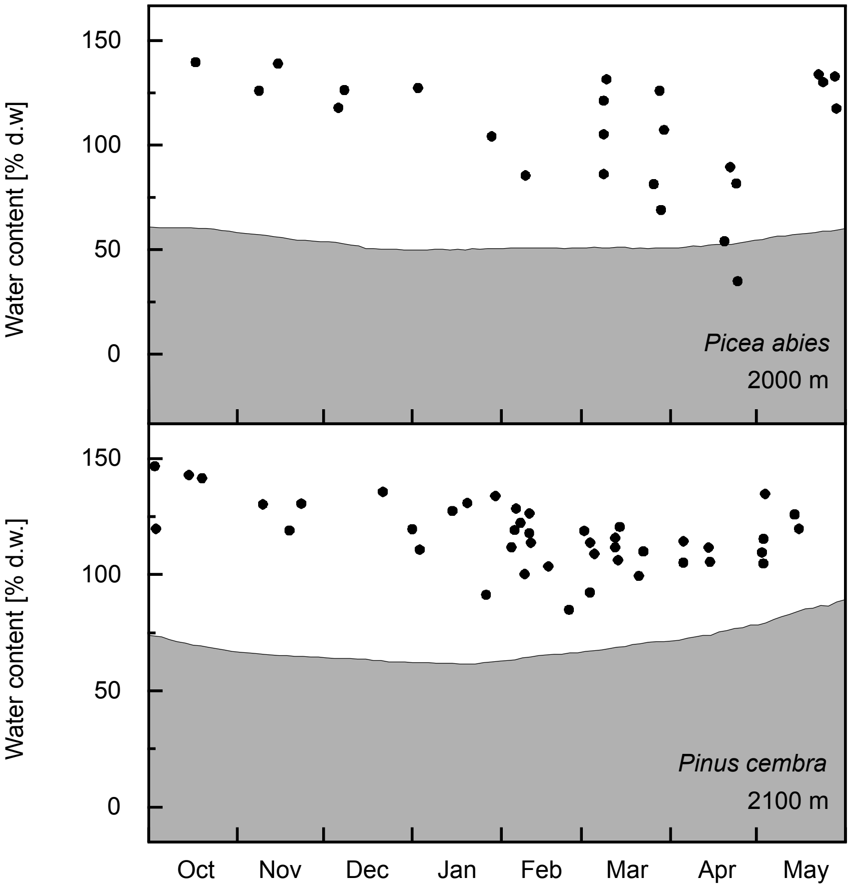

Fig. 8.7. Needle water contents in percent dry weight during several winter seasons. Grey areas indicate water contents causing drought damage, whereby the upper border marks damage of 10 % of the needles. (Modified after Larcher 1972; Platter 1976; Tranquillini 1982.)

Figure 8.7 demonstrates that also *Pinus cembra* hardly reaches critical water deficits during winter, while *Picea abies* cannot totally avoid desiccation injury. In addition to visible drought effects, tree life may be affected by temperature limitations in water uptake and by xylem dysfunction. All these important impairments of plant water relations, although caused by the climatic conditions of alpine winter, may substantially influence tree life in the consecutive summer. The loss of photosynthetic tissues may reduce carbon assimilation and growth of trees, and limitations in water transport may further shorten the already restricted vegetation period.

References

Anfodillo T, Rento S, Carraro V, Furlanetto L, Urbinati C, Carrer M (1998) Tree water relations and climatic variations at the alpine timberline: seasonal changes of sap flux and xylem water potential in *Larix decidua* Miller, *Picea abies* (L.) Karst. and *Pinus cembra* L. Annals of Forest Science 55: 159-172

Anfodillo T, DiBisceglie DP, Urso T (2002) Minimum cuticular conductance and cuticle features of *Picea abies* and *Pinus cembra* needles along an altitudinal gradient in the Dolomites (NE Italian Alps). Tree Physiology 22: 479-487

Aulitzky H (1961) Die Bodentemperaturen in der Kampfzone oberhalb der Waldgrenze und im subalpinen Zirben-Lärchenwald. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 59: 153-208

Badalotti A, Anfodillo T, Grace J (2000) Evidence of osmoregulation in *Larix decidua* at Alpine treeline and comparative responses to water availability of two co-occurring evergreen species. Annals of Forest Science 57: 623-633

Baig MN, Tranquillini W (1976) Studies on upper timberline: morphology and anatomy of Norway spruce (*Picea abies*) and stone pine (*Pinus cembra*) needles from various habitat conditions. Canadian Journal of Botany 54: 1622-1632

Baig MN, Tranquillini W, Havranek WM (1974) Cuticuläre Transpiration von *Picea abies* und *Pinus cembra*- Zweigen auf verschiedener Seehöhe und ihre Bedeutung für die winterliche Austrocknung der Bäume an der alpinen Waldgrenze. Centralblatt für das Gesamte Forstwesen 4: 195-211

Bauer H, Nagele M, Comploj M, Galler V, Mair M, Unterpertinger E (1994) Photosynthesis in cold acclimated leaves of plants with various degrees of frost tolerance. Physiologia Plantarum 91: 403-412

Benecke U, Schulze E-D, Matyssek R, Havranek WM (1981) Environmental control of CO_2-assimilation and leaf conductance in *Larix decidua* Mill. I. A comparison of contrasting natural environments. Oecologia 50: 54-61

Boyce RL, Lucero SA (1999) Role of roots in winter water relations of Engelmann spruce saplings. Tree Physiology 19: 893-898

Boyce RL, Saunders GP (2000) Dependence of winter water relations of mature high-elevation *Picea engelmannii* and *Abies lasiocarpa* on summer climate. Tree Physiology 20: 1077-1086

Christersson L (1972) The transpiration rate of unhardened, hardened and dehardened seedlings of spruce and pine. Physiologia Plantarum 26: 258-263

Christmann A, Havranek WM, Wieser G (1999) Seasonal variation of abscisic acid in needles of *Pinus cembra* L. at the alpine timberline and possible relations to frost resistance and water status. Phyton 39: 23-30

Cochard H, Froux F, Mayr S, Coutand C (2004) Xylem wall collapse in water-stressed pine needles. Plant Physiology 134: 401-408

Giger T, Leuschner C (2004) Altitudinal change in needle water relations of *Pinus canariensis* and possible evidence of a drought-induced alpine timberline on Mt. Teide, Tenerife. Flora 199: 100-109

Gindl W, Grabner M, Wimmer R (2001) Effects of altitude on tracheid differentiation and lignification of Norway spruce. Canadian Journal of Botany 79: 815-821

Goldstein GH, Brubaker LB, Hinckley TM (1985) Water relations of white spruce (*Picea glauca* (Moench) Voss) at tree line in north central Alaska. Canadian Journal of Forest Research 15: 1080-1087

Groß M, Rainer I, Tranquillini W (1991) Über die Frostresistenz der Fichte mit besonderer Berücksichtigung der Zahl der Gefrierzyklen und der Geschwindigkeit der Temperaturänderung beim Frieren und Auftauen. Forstwissenschaftliches Centralblatt 110: 207-217

Günthardt MS, Wanner H (1982) Veränderungen der Spaltöffnungen und der Wachsstruktur mit zunehmendem Nadelalter bei *Pinus cembra* L. und *Picea abies* (L.) Karsten an der Waldgrenze. Botanica Helvetica 92: 47-60

Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. Perspectives in Plant Ecology, Evolution and Systematics 4: 97-115

Hacke UG, Sperry JS, Ewers BE, Ellsworth DS, Schäfer KVR, Oren R (2000) Influence of soil porosity on water use in *Pinus taeda*. Oecologia 124: 495-505

Hadley JL, Smith WK (1983) Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming, U.S.A. Arctic and Alpine Research 15: 127-135

Hadley JL, Smith WK (1986) Wind effects on needles of timberline conifers: seasonal influence on mortality. Ecology 67: 12-19

Hadley JL, Smith WK (1989) Wind erosion of leaf surface wax in timberline conifers. Arctic and Alpine Research 21: 392-398

Hadley JL, Smith WK (1990) Influence of leaf surface wax and leaf area to water content ratio on cuticular transpiration in western conifers USA. Canadian Journal of Forest Research 20: 1306-1311

Häsler R, Streule A, Turner H (1999) Shoot and root growth of young *Larix decidua* in contrasting microenvironments near the alpine treeline. Phyton 39: 47-52

Havranek WM (1972) Über die Bedeutung der Bodentemperatur für die Photosynthese und Transpiration junger Forstpflanzen und die Stoffproduktion an der Waldgrenze. Angewandte Botanik 46: 101-116

Holzer K (1959) Winterliche Schäden an Zirben nahe der alpinen Baumgrenze. Centralblatt für das Gesamte Forstwesen 76: 232-244

Katz C, Oren R, Schulze E-D, Milburn JA (1989) Uptake of water and solutes through twigs of *Picea abies* (L.) Karst. Trees 3: 33-37

Kavanagh KL, Bond BJ, Aitken SN, Gartner BL, Knowe S (1999) Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. Tree Physiology 19: 31-37

Körner Ch (1998) A re-assessment of high elevation treeline positions and their explanation. Oecologia 115: 445-459.

Körner Ch (1999) Alpine plant life: functional plant ecology of high mountain ecosystems, 1st edn. Springer, Berlin, Heidelberg.

Körner Ch, Cochrane PM (1985) Stomatal responses and water relations of *Eucalyptus pauciflora* in summer along an elevational gradient. Oecologia 66: 443-455

Kuuluvainen T, Sprugel DG, Brooks JR (1996) Hydraulic architecture and structure of *Abies lasiocarpa* seedlings in three subalpine meadows of different moisture status a in the Eastern Olympic Mountains, Washington. Arctic and Alpine Research 28: 60-64

Larcher W (1963) Zur spätwinterlichen Erschwerung der Wasserbilanz von Holzpflanzen an der Waldgrenze. Berichte des naturwissenschaftlich medizinischen Vereins Innsbruck 53: 125-137

Larcher W (1972) Der Wasserhaushalt immergrüner Pflanzen im Winter. Berichte der Deutschen Botanischen Gesellschaft 85: 315-327

Larcher W (1985) Winter stress in high mountains. In: Turner H, Tranquillini W (eds) Establishment and tending of subalpine forests: research and management. Eidgenössische Anstalt für das Forstliche Versuchswesen, Ber. 270, pp 11-20

Li C, Liu S, Berninger F (2004) *Picea* seedlings show apparent acclimation to drought with increasing altitude in the eastern Himalaya. Trees 18: 277-283

Lindsay JH (1971) Annual cycle of leaf water potential in *Picea engelmannii* and *Abies lasiocarpa* at timberline in Wyoming. Arctic and Alpine Research 3: 131-138

Martinez-Vilalta J, Sala A, Pinol J (2004) The hydraulic architecture of Pinaceae – a review. Plant Ecology 171: 3-13

Mattes H (1982) Die Lebensgemeinschaft von Tannenhäher und Arve. Eidgenössische Anstalt für Forstliches Versuchswesen Birmensdorf 241: 1-74

Mayr S, Cochard H (2003) A new method for vulnerability analysis of small xylem areas reveals that compression wood of Norway spruce has lower hydraulic safety than opposite wood. Plant, Cell and Environment 26: 1365-1371

Mayr S, Wolfschwenger M, Bauer H (2002) Winter-drought induced embolism in Norway spruce (*Picea abies*) at the alpine timberline. Physiologia Plantarum 115: 74-80

Mayr S, Gruber A, Bauer H (2003a) Repeated freeze-thaw cycles induce embolism in drought stressed conifers (Norway spruce, stone pine). Planta 217: 436-441

Mayr S, Gruber A, Schwienbacher F, Dämon B (2003b) Winter-embolism in a "Krummholz"-Shrub (*Pinus mugo*) growing at the alpine timberline. Austrian Journal of Forest Science 120: 29-38

Mayr S, Rothart B, Dämon B (2003c) Hydraulic efficiency and safety of leader shoots and twigs of Norway spruce trees growing at the alpine timberline. Journal of Experimental Botany 54: 2563-2568

Mayr S, Schwienbacher F, Bauer H (2003d) Winter at the alpine timberline: why does embolism occur in Norway spruce but not in stone pine ? Plant Physiology 131: 780-792

Michaelis P (1934a) Ökologische Studien an der Baumgrenze, IV. Zur Kenntnis des winterlichen Wasserhaushaltes. Jahrbuch für wissenschaftliche Botanik 80: 169-247

Michaelis P (1934b) Ökologische Studien an der Baumgrenze, V. Osmotischer Wert und Wassergehalt während des Winters in den verschiedenen Höhenlagen. Jahrbuch für wissenschaftliche Botanik 80: 337-362

Platter W (1976) Wasserhaushalt, cuticuläres Transpirationsvermögen und Dicke der Cutinschichten einiger Nadelholzarten in verschiedenen Höhenlagen und nach experimenteller Verkürzung der Vegetationsperiode. Ph.D. thesis, Innsbruck University

Richards JH, Bliss LC (1986) Winter water relations of a deciduous timberline conifer, *Larix lyallii* Parl. Oecologia 69: 16-24

Smith WK, Young DR, Carter GA, Hadley JL, McNaughton GM (1984) Autumn stomatal closure in six conifer species of the Central Rocky Mountains. Oecologia 63: 237-242

Sowell JB, Kouitnik DL Lansing AJ (1982) Cuticular transpiration of whitebark pine (*Pinus albicaulis*) within a Sierra Nevadan timberline ecotone, USA. Arctic and Alpine Research 14: 97-103

Sparks JP, Black RA (1998) Winter hydraulic conductivity and xylem cavitation in coniferous trees from upper and lower treeline. Arctic, Antarctic, and Alpine Research 32:397-403

Sparks JP, Campbell GS, Black RA (2001) Water content, hydraulic conductivity, and ice formation in winter stems of *Pinus contorta*: a TDR case study. Oecologia 127: 468-475

Sperry JS, Ikeda T (1997) Xylem cavitation in roots and stems of Douglas-fir and white fir. Tree Physiology 17: 275-280

Sperry JS, Nichols KL, Sullivan JEM, Eastlack SE (1994) Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology 75: 1736-1752

Sperry JS, Sullivan JEM (1992) Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous and conifer species. Plant Physiology 100: 605-613

Tranquillini W (1957) Standortsklima, Wasserbilanz und CO_2-Gaswechsel junger Zirben (*Pinus cembra* L.) an der alpinen Waldgrenze. Planta 49: 612-661

Tranquillini W (1973) Der Wasserhaushalt junger Forstpflanzen nach dem Versetzen und seine Beeinflussbarkeit. Centralblatt für das Gesamte Forstwesen 90: 46-52

Tranquillini W (1974) Der Einfluß von Seehöhe und Länge der Vegetationszeit auf das cuticuläre Transpirationsvermögen von Fichtensämlingen im Winter. Berichte der Deutschen Botanischen Gesellschaft 87: 175-184

Tranquillini W (1976) Water relations and alpine timberline. In: Lange OL, Kappen L, Schulze E-D (eds) Water and plant life. Ecological Studies, vol 19. Springer, Berlin, Heidelberg, New York

Tranquillini W (1979) Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. Ecological Studies, vol 31. Springer, Berlin, Heidelberg, New York

Tranquillini W (1980) Winter desiccation as the cause for alpine timberline. NZFS FRI Technical Paper 70: 263-267

Tranquillini W (1982) Frost drought and its ecological significance. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopaedia of plant physiology 12B, Physiological plant ecology II. Springer, Berlin, Heidelberg, New York, pp 379-400

Tranquillini W, Platter W (1983) Der winterliche Wasserhaushalt der Lärche (*Larix decidua* Mill.) an der alpinen Waldgrenze. Verhandlungen Gesellschaft für Ökologie 9: 433-443

Turner H (1961) Jahresgang und biologische Wirkung der Sonnen- und Himmelsstrahlung an der Waldgrenze der Ötztaler Alpen. Wetter und Leben 13: 93-113

Tyree MT, Davis SD, Cochard H (1994) Biophysical perspectives of xylem evolution: Is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? IAWA Journal 15: 335-360

Van Gradingen P, Grace J, Jeffree CE (1991) Abrasive damage by wind to the needle surface of *Pinus sylvestris* L. and *Picea sitchensis* (Bong.) Carr. Plant, Cell and Environment 14: 185-193

Wardle P (1981) Winter desiccation of conifer needles simulated by artificial freezing. Arctic and Alpine Research 13: 419-423

Wieser G (2000) Seasonal variation of leaf conductance in a subalpine *Pinus cembra* during the winter months. Phyton 40: 185-190

Wieser G (2002) Exchange of trace gases at the tree - atmosphere interface: ozone. In: Gasche R, Papen H, Rennenberg H (eds) Trace gas exchange in forest ecosystems. Tree Physiology, vol 3. Kluwer Academic Publishers, Dordrecht, Boston, London, pp 211-226

Zimmermann MH (1978) Hydraulic architecture of some diffuse-porous trees. Canadian Journal of Botany 56: 2286-2295

Zimmermann MH (1983) Xylem structure and the ascent of sap. Springer Verlag, Berlin.

Zweifel R, Häsler R (2000) Frost-induced reversible shrinkage of bark of mature subalpine conifers. Agricultural and Forest Meteorology 102: 213-222

9 Phytopathogens at the Alpine Timberline

Helmut Bauer[1] and Christian Schwaninger[2]

[1]Institut für Botanik, Universität Innsbruck
[2]Abteilung Waldschutz, Tiroler Landesregierung, Innsbruck

9.1 Introduction

Harsh conditions at the timberline ecotone may reduce the defence power of trees, which consumes a lot of energy (Herms and Mattson 1992). On the other hand, low temperatures may also restrict phytopathogenic activity. Thus, phytopathogenic impact on trees at high elevation should not be particularly serious. For example, Smith and Hoffman (2001) reported an even negative correlation between elevation and the presence and the intensity of disease by the white pine blister rust (*Cronartium ribicola*). However, for the timberline ecotone of the European Alps almost no information on specific effects on functions, growth, and mortality upon phyotpathogenic attacks on trees is available. Therefore, we can only present a tentative list of the most important fungal pests occurring at the alpine timberline. Furthermore, we deal with the effects of the needle rust *Chrysomyxa rhododendri* whose occurrence is restricted to the timberline and whose effects were extensively studied by our group.

9.2 Fungal pathogens at the alpine timberline

Table 9.1 gives a survey of some fungal pathogens with the type of disease, an assessment of their risk and their relevance for afforesting high elevation sites in Tyrol.

G. Wieser and M. Tausz (eds.), Trees at their Upper Limit, 163–170.

Table 9.1. The most important fungal phytopathogens of timberline trees and their relevance for natural re-establishment and afforestation in European Alps.

Fungal germ	Disease	Attacked tree species	Relevance for natural re-establishment	Relevance for afforestation
Chrysomyxa abietis	Needle bladder rust “Fichtennadelblasenrost”	*Picea abies*	less extensive than *Ch. rhododendri*	
Chrysomyxa rhododendri	Needle bladder rust “Fichtennadelblasenrost”	*Picea abies*	Selective effects	high risk
Encoeliopsis laricina	Shoot dieback “Triebsterben”	*Larix decidua*	endangered near afforestations	high risk
Gremmeniella abietina	Shoot dieback “Triebsterben”	*Pinus nigra* *P. mugo* *P. cembra* *P. sylvestris*	high risk for *P. cembra*	high risk for *P. cembra*
Herpotrichia coulteri	Black snow mould fungus “Schwarzer Schneeschimmel”	*Pinus mugo*	selective effects at snowy sites	
Herpotrichia juniperi = *Herpotrichia nigra*	Black snow mould fungus “Schwarzer Schneeschimmel”	*Picea abies*	selective effects at snowy sites very probable	on sites out of natural places for *P. abies*
Lophodermium pinastri	“Kiefernschütte“	*Pinus mugo*	weakness parasite (“Schwächeparasit”)	lethal for individual specimen
Lophodermium sulcigena	„Schwedische Kiefernschütte“	*Pinus mugo*	seldom lethal	
Phacidium infestans	“Schneeschütte”	*Pinus cembra*	high risk at snowy sites	high risk at snowy sites

9.3 Effects of the needle rust *Chrysomyxa* on Norway spruce

Chrysomyxa rhododendri is a needle rust requiring a host shift between *Rhododendron* species (telio-host) and Norway spruce (intermediate aecio-host) for completion of its life cycle (De Bary 1879). Infection of spruce is therefore restricted to subalpine regions where trees are within the reach of the airborne basidiospores formed on *Rhododendron* leaves in late spring. Basidiospores only penetrate into developing current-year needles of spruce. During early summer, infected needles show a typical yellow discoloration (Fig. 9.1) as a consequence of chlorophyll breakdown and carotenoid formation by the fungus (Pfeifhofer 1989; Bauer et al. 2000). In mid summer, after development of aeciospores in aecia, infected needles form an abscission zone at their base and are shed. Hence, attacked shoots often become completely bare.

Fig. 9.1. Twigs of *Picea abies* whose current-year shoots are infected by *Chrysomyxa rhododendri*.

Some parameters related to photosynthesis in *Chrysomyxa*-infected and control plants are compiled in Table 9.2. Loss of chlorophyll in infected needles is accompanied by characteristic changes in most parameters of fluorescence of chlorophyll *a*.

Table 9.2. Some parameters related to photosynthesis in *Chrysomyxa*-infected needles expressed as percentage of values in non-infected trees. Values are expressed per unit leaf area if not stated otherwise. (Data from Bauer et al. 2000; Mayr et al. 2001; and unpublished data from H. Bauer and U. Oberbacher.)

Parameter	Young trees (3-4 years old)	Adult trees (50-60 years old)
Chlorophyll a+b	17	24
Fluorescence (F_V/F_M)	65	58
Photosynthetic electron transport		
PS II		14
per unit chlorophyll a+b		62
PS I		29
per unit chlorophyll a+b		131
O_2 evolution		
current year needles	12	
per unit chlorophyll a+b	70	
older needles (not infected)	148	
CO_2 uptake		
current year needles		53
per unit chlorophyll a+b		101
older needles (not infected)		133
Dark respiration	258	
Gross photosynthesis	16	
per unit chlorophyll a+b	149	
Soluble carbohydrates		
current year leaves	61	
older leaves (not infected)	48	

Thereby, PS II centres are inactivated leading to a reduced electron transport through PS II in isolated thylakoids, but in PS I the rate per unit chlorophyll is not affected. During the infection the overall photosynthetic process breaks down, as demonstrated by measurements of O_2 evolution at saturated CO_2 concentration or CO_2 uptake at ambient CO_2. Dark respiration is strongly stimulated in infected needles, but this is not sufficient to explain the reduction in net photosynthesis. This is mainly due to the loss of the photosynthetic machinery as indicated by the only minor reduction of gas exchange when expressed per unit chlorophyll. Older needles cannot be infected by *Chrysomyxa* and are able to react to the loss of the new flush. Photosynthetic capacity of 1- and 2-year old needles of infected spruce trees increased by up to 50% compared with needles of the same age class on trees not infected by *Chrysomyxa* (Table 9.2).

Photosynthetic impairment leads to a shortage of carbohydrates in all organs of infected trees (Table 9.2). Hence, dry matter production is clearly reduced (Fig. 9.2). As in young trees the portion of the youngest needle age class on the whole foliage is very high, loss of current-year needles by *Chrysomyxa* infection is quite detrimental for the establishment of seedlings. Thus, natural rejuvenation or afforestation is seriously impaired in regions where *Rhododendron* species are widespread. In adult trees current-year needles contribute only a minor part to the carbon acquisition of the whole tree (Schulze et al. 1977). However, *Chrysomyxa* infection could be detected by analysing radial growth of adult trees after heavy infections (Oberhuber et al. 1999; Mayr et al. 2001; Fig. 9.3) Furthermore, height growth is significantly negatively correlated with the degree of infection (A. Gruber and H. Bauer unpublished; Fig. 9.4).

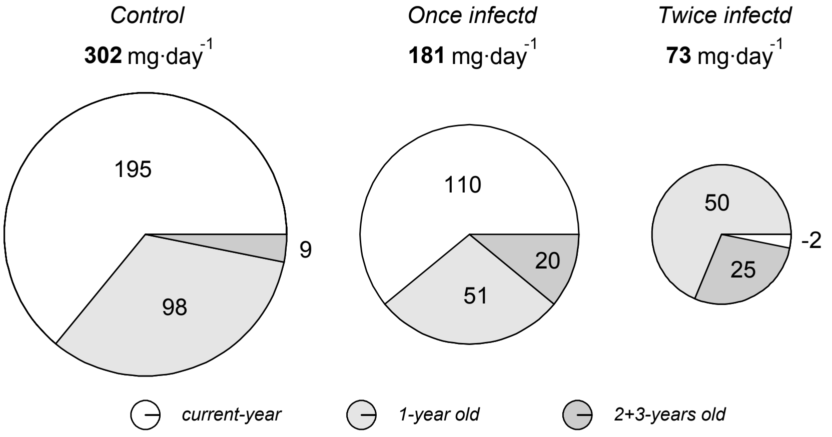

Fig. 9.2. Dry matter production of 4-years old Norway spruce seedlings variously infected by *Chrysomyxa*. Values are estimated from biomass and photosynthetic capacity of the different needle age classes. (Data from Plattner et al. 1999.)

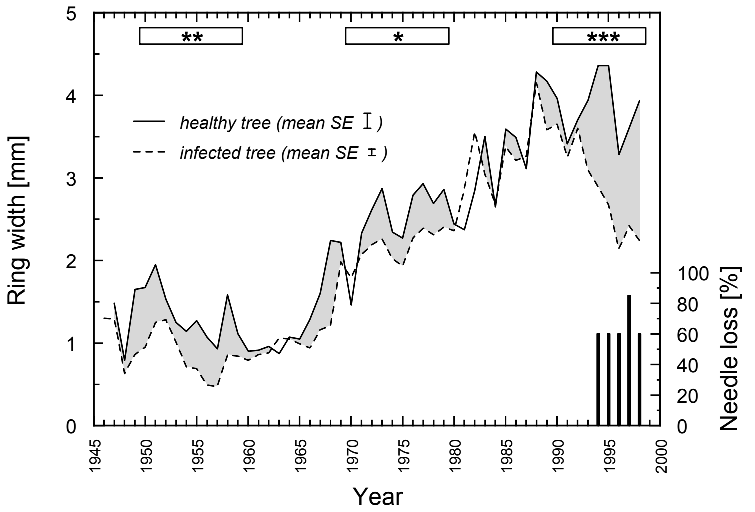

Fig. 9.3. Ring width series of a healthy (solid line) and an infected tree growing side by side at 1700 m in Tyrol. Infection intensities of the infected tree (1994-1998) are indicated by the percentage of needle loss. Bars marked with asterisks indicate significant differences of mean radial growth within 10 year intervals at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively. (From Mayr et al. 2001.)

Sometimes a single Norway spruce specimen, which is hardly infected by *Chrysomyxa* can be found among surrounding trees that show serious symptoms of disease. The reasons for the specific resistance are not clear. We could not find any differences between healthy and infected trees in the amount and composition of phenolic compounds and in the thickness of cuticle. As healthy trees were observed to develop the new flush later in spring, it is possible that they escape infection during the period of highest basiodiospore densities (A. Kohne and H. Bauer unpublished).

As stated above, trees at the timberline are hardly more endangered by phytopathogens than trees at low elevation. Therefore, pathogens are certainly not responsible for high elevation limits of trees. However, the species composition at the treeline may be modulated by the occurrence of specific pathogens. For instance, in some valleys of the Central Alps the treeline on east-exposed slopes, where *Rhododendron* species are missing, is formed by Norway spruce, whereas on west-exposed slopes, where *Rhododendron* is widespread, *Pinus cembra* is dominant. Here, Norway spruce is very probably impaired by *Chrysomyxa* and not able to compete (cf. Gams 1970). However, microclimatic and edaphic factors might support the specific dominance of these species at the alpine timberline.

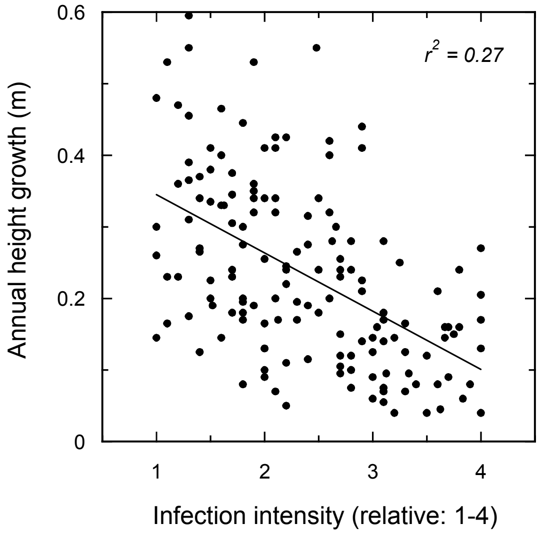

Fig. 9.4. Correlation between height growth and degree of infection with *Chrysomyxa* derived from needle loss during the last five years (A. Gruber and H. Bauer, unpublished.)

References

Bauer H, Plattner K, Volgger W (2000) Photosynthesis in Norway spruce seedlings infected by the needle rust *Chrysomyxa rhododendri*. Tree Physiology 20: 211-216

De Bary A (1879) *Aecidium abietinum*. Botanische Zeitung 37: 761-847

Gams H (1970) Die Erforschung der Floren- und Vegetationsgeschichte der Ötztaler Alpen. Mitteilungen der Ostalpin-Dinarischen Gesellschaft für Vegetationskunde 11: 55-62

Herms DA, Mattson WJ (1992) The dilemma of plants: To grow or defend. Quarterly Review of Biology 67: 283-335

Mayr S, Siller C, Kriss M, Oberhuber W, Bauer H (2001) Photosynthesis in rust-infected adult Norway spruce in the field. New Phytologist 151: 683-689

Oberhuber W, Thomaser G, Mayr S, Bauer H (1999) Radial growth of Norway spruce infected by *Chrysomyxa rhododendri*. Phyton 39: 147-154

Pfeifhofer HW (1989) On the pigment content of Norway spruce needles infected with *Chrysomyxa rhododendri* and the carotenoids of the fungus aeciospores. European Journal of Forest Pathology 19: 363-369

Plattner K, Volgger W, Oberhuber W, Mayr S, Bauer H (1999) Dry mass production in seedlings of Norway spruce infected by the needle rust *Chrysomyxa rhododendri*. European Journal of Forest Pathology 29: 365-370

Schulze E-D, Fuchs MI, Fuchs M (1977) Spacial distribution of photosynthetic capacity and performance in a mountain spruce forest of northern Germany 1.Biomass distribution and daily CO_2 uptake in different crown layers. Oecologia 29: 43-61

Smith JP, Hoffman JT (2001) Site and stand characteristics related to white pine blister rust in high-elevation forests of southern Idaho and western Wyoming. Western North American Naturalist 61: 409-416

10 Frost Resistance at the Upper Timberline

Gilbert Neuner

Institut für Botanik, Universität Innsbruck

10.1 Introduction

In the timberline ecotone, above the forest limit, damage to buds, leaves and shoots tends to increase rapidly with increasing altitude (Tranquillini 1979). Depending on their intensity, duration and variability, climate extremes impair the vital functions and set the distributional limits of plant species. Within a given habitat, the possibility of survival of a species generally increases with the resistance of the most vulnerable vital part of the plant. Resistance against biotic or abiotic extremes is the net result of tolerance and avoidance (Levitt 1972; Larcher 1980, 2001) or if damage is met by an adequate recuperation capacity. Extraordinary unfavourable conditions (≅ stress, sensu Larcher 1987) are important components of life. They can be both a threat and a driving force for adaptation, modulation and resistance. Therefore, resistance, adaptation, and stress have to be seen in a conceptual framework.

This chapter will focus on direct low temperature effects. Side effects of freezing such as frost drought which is not restricted to the timberline ecotone have been considered in Chap. 8. Mechanical damage by wind, ice blasting, snow break and avalanches is only of small scale, local importance and has been discussed briefly in Chap. 1.

G. Wieser and M. Tausz (eds.), Trees at their Upper Limit, 171–180.

10.2 Frost damage

Freezing temperatures are generally an important filter on plant recruitment, survival, productivity and geographic distribution (Sakai and Larcher 1987) and can have dramatic impacts on plants at cellular to ecosystem scales (Loik et al. 2004). At the temperate treeline freezing temperatures may, in combination with other environmental factors, produce various types of freezing related injuries such as winter desiccation or photo-destruction. However, frost damage is the direct and most evident harmful effect of freezing temperatures *per se*. The risk of frost damage depends on the difference between freezing temperatures and frost resistance during certain parts of the year. At the temperate treeline the risk of frost damage must be considered low during winter but high during the growing season when plants are exposed to unpredictable subfreezing temperatures in the form of freeze-thawing cycles.

10.2.1 Winter

Winter temperatures below -40 °C are not uncommon in the Northern Hemisphere (Zwiazek et al. 2001). In European Alpine areas air temperature minima may drop down to -36 °C during winter (> 2000 m, Tyrol, Austria; Central Institute for Meteorology and Geodynamics, Austria). Because of temperature inversion, treeline trees are not necessarily exposed to lower air temperatures than lowland trees. However, in subalpine environments, due to increased radiation at night, leaves of conifers may be as much as 9.3 °C colder than air (Tranquillini 1958; 3-8 °C: Jordan and Smith 1994). Hence, in extreme cases leaf temperatures down to -45.3 °C could be possible. In the artificially fully frost hardened state maximum winter frost resistance of leaves of European Alpine treeline tree species varies considerably ranging from -45 °C to -90 °C (Table 10.1). Frost resistance either distinctly exceeds (*Larix decidua, Pinus cembra, Pinus mugo*) or at least equals (*Picea abies*) the potential leaf temperature extreme. Maximum frost resistances of trees found under natural frost hardening at the treeline were much lower: -38 to -48 °C (LT_i). Nevertheless the difference between frost resistance and the actual freezing temperature was usually between 27 and 29 K but ranged from 15 to 40 K in midwinter. Hence, the risk of frost damage during winter at the alpine treeline appears to be low as already suggested by Tranquillini (1979) at least for the frost hardiest species. The results for leaves also hold true for buds as buds from conifers of the coldest climatic zones tend to have a frost resistance that is equal to or a bit less than that of their leaves (Bannister and Neuner 2001).

Table 10.1. Maximum winter frost resistance ($LT_{0\text{-}i}$, LT_{50}) of leaves of European treeline tree species obtained after artificial frost hardening or during midwinter after natural frost hardening at the treeline. Mean, minimum and maximum temperature difference between actual air temperature minimum and the temperature of initial frost damage (ΔT) observed after natural frost hardening in midwinter. (Data from: Ulmer 1937; Pisek and Schiessl 1946; Tranquillini 1958; Schwarz 1970.)

Species	Maximum winter frost resistance after		Mean ΔT (K) (min/max)
	artificial frost hardening	natural frost hardening	
Larix decidua	-70^{e}		
Picea abies	*-45*^{a}/-50^{e}	-38^{c,f,h}/-39^{d}/*45*^{d}	26.8±5.1 (20/36)
Pinus cembra	*-80*^{a}/-90^{e}	-42^{h}/*-43*^{f}/-44^{f}/-48^{c}/*-54*^{b}	29.2±5.9 (15/40)
Pinus mugo	-90^{e}	-35^{c,h}	

[a]Bauer et al. 1994 (LT_{50}), [b]Christmann et al. 1999 (LT_{50}), [c]Pisek and Schiessl 1946 (LT_{i}), [d]Pümpel et al. 1975 ($LT_{i,}$, LT_{50}), [e]Sakai and Okada 1971 (LT_{0}), [f]Schwarz 1970 (LT_{50}), [g]Tranquillini 1958 (LT_{i}), [h]Ulmer 1937 (LT_{i})

The establishment of tree seedlings and young plants may even be favoured in the treeline ecotone as they are usually covered by snow during winter and thus exposed to only moderate temperatures around 0 °C. Snow buried woody plants, however, are often less frost resistant (6-10 K; Tranquillini 1958; Schwarz 1970; Neuner et al. 1999) than exposed plants. Frost damage to such plants (e.g. snow covered *Pinus cembra* (LT_{i}): -31 °C; air temperature minimum: -30.6 °C; Tranquillini 1958) might occur when they are suddenly blown free of snow during cold spells (Tranquillini 1979).

10.2.2 Frost hardening capacity

Frost survival depends not only on the extent of frost resistance but even more importantly on adequate timing of frost hardening. During autumn and winter woody plants show a fast response to frost hardening treatments with some hardening within 1 to 2 days and full hardening reached within 4 to 10 days. The rate of frost hardening is known to be slowest during the dehardening period in spring (Larcher 1985).

Winter frost damage has generally been assumed to be unlikely for plants growing in their natural environment (Sakai and Larcher 1987) as during periods with predictable cold weather (winter) frost hardening usually provides sufficient protection from frost damage. However, plants may be at risk if frost dehardening occurs early during unnaturally warmer periods in winter. A 4 °C rise in winter temperature significantly accelerates the frost dehardening process in several Northern Hemisphere woody plants, such as Scots pine (Repo et al. 1996), bilberry (Taulavuori et al. 1997) and mountain birch (Taulavuori et al. 2004). These findings suggest an increase in the risk of frost damage in late winter or spring.

10.2.3 Summer

In contrast to lowlands, freeze-thawing cycles can occur during the whole growing season in the treeline ecotone causing unpredictable subfreezing temperatures. In particular, late spring frosts in June are a real threat causing recurrent frost damage to new shoots of subalpine woody plant species (Taschler et al. 2004; Taschler and Neuner 2004). As early as 1869 Kerner described 100 % frost damage to new needles of *Picea abies* at the treeline ecotone (about 2100 m a.s.l.) at the end of June. Similar frost damage to the new shoots of a range of woody subalpine species was observed after night frosts in June 1999 and 2002 at the same site (Fig. 10.1; pers. obs. Neuner).

Fig. 10.1. Frost damage to new sprouts of (**A, B**) *Picea abies* and (**C**) *Larix decidua* after a night frost of -2.6 °C (air temperature) on 23. 6. 1999 at 2100 m a.s.l.. (A) Two individual spruce trees growing in close proximity showed completely different frost damage. The new sprouts of one tree (left) remained undamaged while in the second tree (right) this year's annual flush was 100% frost damaged. The two individuals experienced the same night frost but showed a completely different level of damage due to the different developmental stage of their new sprouts.

These observations underline the significance of frost damage to young shoots of tree species at the treeline in the Central European Alps. Although recurrent frost damage did not appear to threaten survival of trees, partial injury appeared to contribute to the distorted growth of trees in the krummholz belt (Däniker 1923; Wardle 1968; Holzer 1970; Tranquillini 1979; Sakai and Larcher 1987; Gross et al. 1991).

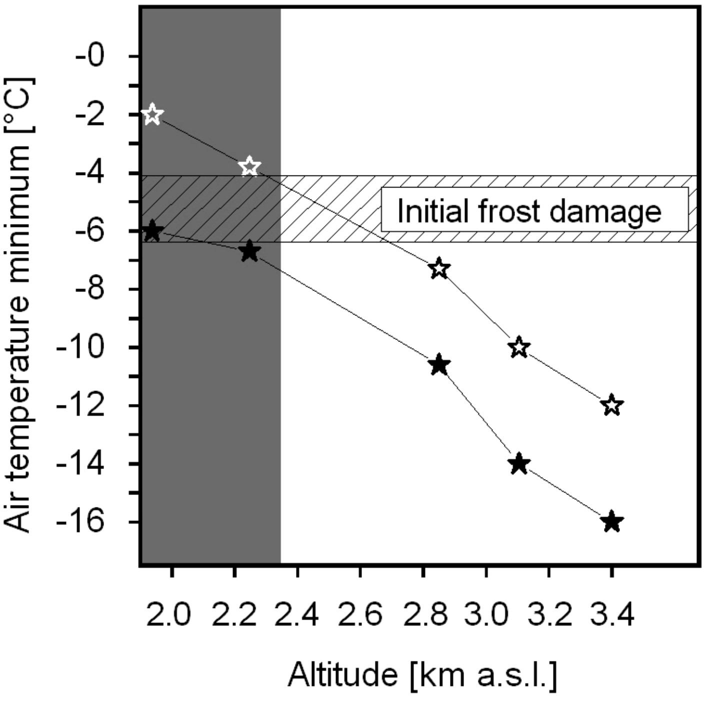

Fig. 10.2. Absolute air temperature minima (5-40 years) in June (solid star) and in July and August (open star) at different altitudes between 1938 and 3400 m. Temperature data were provided by ZAMG Austria and derived from various climate stations (Obergurgl 1938 m (40 years), Patscherkofel 2247 m (30 years), Pitztaler Gletscher 2850 m (8 years), Sonnblick 3105 m (40 years), Brunnenkogel 3400 m (5 years)). Treeline in the Central European Alps is located at 2350 m (altitudes below this are shaded grey). Initial frost damage (LT_i) in new sprouts of treeline trees (*Larix decidua, Picea abies, Pinus cembra, Sorbus aucuparia*) occurs between -3.8 and -6.3 °C and is indicated by the hatched bar.

Frequent frost damage to new shoots from late frosts is also reported to occur at the upper treeline in New Zealand (Wardle 1965). At the subarctic treeline freezing injuries in summer also play a decisive role in the development and growth of adult conifer trees, e.g. causing mat growth forms of *Picea mariana* (Sutinen et al. 2001). Freezing injuries to new shoots are not a specific feature of treelines but can be observed all over the northern distribution area of conifers (Sutinen et al. 2001). However, at high elevation the extent and frequency of frost events increases significantly (Fig. 10.2). While below the treeline damaging frost may occur only in June, above the treeline freezing temperatures capable of producing frost damage in new leaves are possible throughout the summer. Frost damage above the treeline may thus be not only more likely but also occurs more often.

As early as 1969, Holzer reported that the extent of spring frost damage in new sprouts of *Picea abies* in an alpine provenance test was higher in early flushing provenances. However, this is only partly true as significant changes in frost resistance occur during development of new sprouts (Fig. 10.3; Taschler et al. 2004; Taschler and Neuner 2004) and after full expansion earlier flushing individuals may remain completely undamaged while later flushing individuals are 100 % frost damaged (see Fig. 10.1A). The extent of a freezing event and its timing are both decisive factors in the occurrence of frost damage due to significant changes in frost resistance during sprouting. After bud break during initial leaf expansion (0 – 60 % of final size) new sprouts are most frost susceptible. Frost hardening during expansion of new sprouts seems unlikely. Sprouting leaves of timberline tree species are significantly frost hardier than leaves of lowland tree species such as *Carpinus betulus* and *Ulmus minor*. Among the treeline tree species, *Picea abies* is not only more frost susceptible during leaf expansion than the other species, but due to earlier sprouting *Picea abies* is at higher risk of frost damage. Loss of new sprouts is particularly severe in conifers at the treeline as re-growth is usually not observed until the next year.

10.2.4 Rate of temperature change

Rapid thawing can damage foliage. The elevated mountain horizon delays sunrise. While the direct sunlight can come late, its arrival is sudden and it is already intense. This can cause very high rates of thawing for frozen needles (maximum 2 °C min^{-1}; Tranquillini 1979). In such situations in the treeline ecotone, needles of *Pinus cembra* on the southeast side of isolated tree crowns can be seriously damaged (Holzer 1959).

It has long been known that rapid freezing can increase frost damage in artificially frozen samples (Pisek and Schiessl 1946). Average cooling and thawing rates of 13 °C h^{-1} with maxima up to 125 to 140 °C h^{-1} are possible in the treeline ecotone (Gross 1989; Gross et al. 1991). Although it is possible that frost damage in the treeline ecotone occurs due to rapid cooling rates below 0 °C, direct evidence is not yet available.

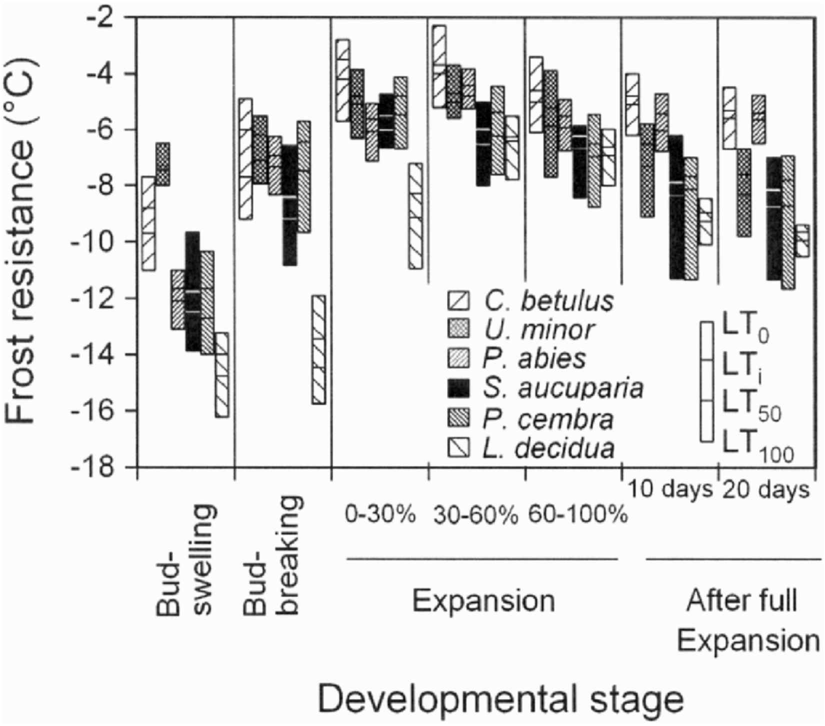

Fig. 10.3. Changes in frost resistance measured *in situ* during sprouting in lowland (*Carpinus betulus* -900 m a.s.l., *Ulmus minor* -700 m a.s.l.) and timberline tree species (*Larix decidua* -2400 m a.s.l., *Picea abies* -2400 m, *Pinus cembra* -2400 m, *Sorbus aucuparia* -2400 m a.s.l.). LT_x, damage degree in %; n= 45. (Data from Taschler 2003, Taschler et al. 2004, Taschler and Neuner 2004.)

References

Bannister P, Neuner G,. (2001) Frost resistance and the distribution of conifers. In: Bigras FJ, Colombo SJ (eds) Conifer cold hardiness. Kluwer Academic Publishers, Dordrecht, Boston, London, pp 3-22.

Bauer H, Nagele M, Comploj M, Galler V, Mair M, Unterpertinger E (1994) Photosynthesis in cold acclimated leaves of plants with various degrees of freezing tolerance. Physiologia Plantarum 91: 403-412

Christmann A, Havranek W, Wieser G (1999) Seasonal variation of abscisic acid in needles of *Pinus cembra* L. at the alpine timberline and possible relations to frost resistance and water status. Phyton 39: 23-30

Däniker A (1923) Biologische Studien über Baum- und Waldgrenzen, insbesondere über die klimatischen Ursachen und deren Zusammenhänge. Vierteljahresschrift der Naturforschenden Gesellschaft in Zürich 68: 1-102

Gross M (1989) Untersuchungen an Fichten der alpinen Waldgrenze: Dissertationes Botanicae 139. Kramer Berlin, Stuttgart

Gross M, Rainer I, Tranquillini W (1991) Über die Frostresistenz der Fichte mit besonderer Berücksichtigung der Zahl der Gefrierzyklen und der Geschwindigkeit der Temperaturänderung beim Frieren und Auftauen. Forstwissenschaftliches Centralblatt 110: 207-217

Holzer K (1959) Winterliche Schäden an Zirben nahe der alpinen Baumgrenze. Zentralblatt für das Gesamte Forstwesen. 76: 232-244

Holzer K (1969) A late frost injury in an alpine Norway spruce (*Picea abies* L. Karst.) provenance test. Sec. World Consultation on Forest Tree Breeding. Washington

Holzer K (1970) Cold resistance in spruce Sec. World Consultation on Forest Tree Breeding. Documents, vol 1. Washington, pp 597-613

Jordan DN, Smith WK (1994) Energy balance analysis of nighttime leaf temperatures and frost formation in a subalpine environment. Agricultural and Forest Meteorology 71: 359-372

Kerner A (1869) Abhängigkeit der Pflanzengestalt von Klima und Boden. Festschriften der Versammlungen Deutscher Naturforscher und Ärzte, Bd. 6: 29-45

Larcher W (1980) Klimastreß im Gebirge – Adaptationstraining und Selektionsfilter für Pflanzen. Rheinisch-Westfälische Akademie der Wissenschaften, Vorträge 291: 49-88

Larcher W (1985) Kälte und Frost. In: Sorauer P (ed) Handbuch der Pflanzenkrankheiten, 7th edn, part 5. Parey, Berlin, pp 107-320

Larcher W (1987) Stress bei Pflanzen. Naturwissenschaften 74: 158-167

Larcher W (2001) Ökophysiologie der Pflanzen: Leben, Leistung und Streßbewältigung der Pflanzen in ihrer Umwelt. Ulmer, UTB, Stuttgart

Levitt J (1972) Response of plants to environmental stresses. Academic Press, New York, London

Loik ME, Still CJ, Huxman TE, Harte J (2004) In situ photosynthetic freezing tolerance for plants exposed to a global warming manipulation in the Rocky Mountains, Colorado, USA. New Phytologist 162: 331-341.

Neuner G, Ambach D, Buchner O (1999) Readiness to frost harden during the dehardening period measured in situ in leaves of *Rhododendron ferrugineum* L. at the alpine timberline. Flora 194: 289-296

Pisek A, Schiessl R (1946) Die Temperaturbeeinflussbarkeit der Frosthärte von Nadelhölzern und Zwergsträuchern an der alpinen Waldgrenze. Berichte des naturwissenschaftlich-medizinischen Vereins Innsbruck 47: 33-52

Pümpel B, Göbl F, Tranquillini W (1975) Wachstum, Mykorhiza und Frostresistenz von Fichtenjungpflanzen bei Düngung mit verschiedenen Stickstoffgaben. European Journal of Forest Pathology 5: 83-97

Repo T, Hänninen H, Kellomäki S (1996) The effects of long-term elevation of air temperature and CO_2 on the frost hardiness of Scots pine. Plant, Cell and Environ 19: 209-216

Sakai A, Larcher W (1987) Frost survival of plants. Responses and adaptation to freezing stress. Ecological Studies, vol 62. Springer, Berlin Heidelberg New York

Sakai A, Okada S (1971) Freezing resistance in conifers. Silvae Genetca 20: 91-97

Schwarz W (1970) Der Einfluss der Photoperiode auf das Austreiben, die Frosthärte und die Hitzeresistenz von Zirben und Alpenrosen. Flora 159: 258-285

Sutinen LM, Arora R, Wisniewski M, Ashworth E, Strimbeck R, Palta J (2001) Mechanisms of frost survival and freeze-damage in nature. In: Bigras FJ, Colombo SJ (eds) Conifer cold hardiness. Kluwer Academic Publishers, Dordrecht, Boston, London, pp 89-120

Taschler D (2003) Eisbildung und Frostresistenz in Blättern während der Vegetationsperiode. Ph.D thesis, Innsbruck University

Taschler D, Neuner G (2004) Summer frost resistance and freezing patterns measured in Situ in leaves of major alpine plant growth forms in relation to their upper distribution boundary. Plant, Cell and Environment 27: 737-746

Taschler D, Beikircher B, Neuner G (2004) Frost resistance and ice nucleation in leaves of five woody timberline species measured in Situ during shoot expansion. Tree Physiology 24: 331-337

Taulavuori K, Laine K, Taulavuori E, Pakonen T, Saari E (1997) Accelerated dehardening in Bilberry (*Vaccinum myrtillus* L.) induced by a small elevation in air temperature. Environmental Pollution 98: 91-95

Taulavuor KMJ, Taulavuori EB, Skre O, Nilsen J, Igel B, Laine KM (2004) Dehardening of mountain birch (*Betula pubescent Sap czerepanovii*) ecotypes at elevated winter temperatures. New Phytologist 162: 427-436

Tranquillini W (1958) Die Frosthärte der Zirbe unter besonderer Berücksichtigung autochtoner und aus Forstgärten stammender Jungpflanzen. Forstwissenschaftliches Centralblatt 77: 89-105

Tranquillini W (1979) Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. Ecological Studies, vol 31. Springer, Berlin, Heidelberg, New York

Ulmer W (1937) Über den Jahresgang der Frosthärte einiger immergrüner Arten der alpinen Stufe, sowie Zirbe und Fichte. Jahrbuch für wissenschaftliche Botanik 84: 553-592

Wardle P (1965) A comparison of alpine timberlines in New Zealand and North America. New Zealand Journal of Botany 3: 113-135

Wardle, P (1968) Engelmann spruce (*Picea endelmanii* ENGEL.) at its upper limits on the Front Range, Colorado. Ecology 49: 483-495

Zwiazek JJ, Renault S, Croser C, Hansn J, Beck E (2001) Biochemical and biophysical changes in relation to cold hardiness. In: Bigras FJ, Colombo SJ (eds) Conifer cold hardiness. Kluwer Academic Publishers, Dordrecht, Boston, London, pp 165-186

11 Photo-Oxidative Stress at the Timberline

Michael Tausz

School of Forest and Ecosystem Science, University of Melbourne

11.1 Introduction

Environmental conditions at the alpine timberline present stress factors, which potentially limit tree growth. According to Elstner and Oßwald (1994) “stress” in plants is generally characterised by the increased formation of reactive oxygen species (ROS) in the cells. Sources of these toxic ROS are mainly electron transport chains, such as in photosynthesis or respiration (Foyer and Noctor 2000). Since a certain amount of ROS is also formed under non-stress conditions, plants have evolved protective mechanisms - the antioxidative defence systems - to keep ROS under control. This chapter will explore the role of ROS and antioxidants in limiting tree growth at the alpine timberline.

11.2 Mechanisms of ROS production in green plant cells under stress

The major pathway of stress-related ROS production in green plant cells results from an imbalance between the amount of absorbed light energy and the consumption rate of the reductant NADPH in the photosynthetic apparatus of the chloroplast (Fig. 11.1), a situation often referred to as “photo-oxidative stress” (Foyer and Noctor 2000). In such circumstances, energy is absorbed in excess of what is needed to drive electron transport and carbon fixation. Such excess excitation energy can be transferred directly to molecular oxygen (producing the highly reactive singlet oxygen)

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or leads to an over-reduction of the electron transport chain causing electrons to “leak” to acceptors other than NADP, mainly to molecular oxygen (O_2). A variety of ROS, among them singlet oxygen (excited dioxygen, $^1O_2$), the hydroxyl free radical ($OH^{\cdot}$), the superoxide anion free radical ($O_2^{\cdot-}$), or hydrogen peroxide (H_2O_2), are formed (Elstner and Oßwald 1994). These ROS are highly reactive and, if not kept under control, initiate pigment bleaching, lipid peroxidation, protein oxidation, or oxidative damage to nucleic acids.

Many different environmental impacts can induce or increase the imbalance between the light and dark reactions of photosynthesis. Drought conditions, for example, will lead to stomatal closure limiting CO_2 uptake and therefore limit carbon fixation rate. Low temperatures will slow down the enzymatic reactions of the Calvin cycle, but hardly affect the membrane bound electron transport and light capture (Fig. 11.1).

In addition to such internal mechanisms of ROS formation, certain chemicals or impacts lead to a more direct production of ROS. Two better studied examples shall be mentioned here:

(1) Ozone (O_3), a major oxidative atmospheric trace gas, is a reactive oxygen species in itself. It is taken up by plants mainly via the stomata. Once inside the leaf, it reacts with components in the cell walls and outer cell membranes and leads to the formation of secondary products, among them other ROS. In spite of a large body of literature on O_3 effects on plants, the details of the damaging mechanisms are still unclear, but ROS certainly play an important role.

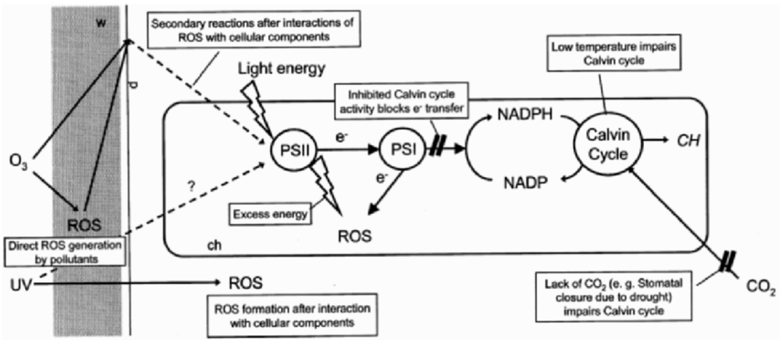

Fig. 11.1. Simplified scheme of effects of stress factors on primary processes of photosynthesis and pathways of stress-related reactive oxygen (ROS) formation in chloroplasts. PSI, PSII photosystem I and II, w cell wall, p plasmalemma, ch chloroplast, CH carbohydrates.

(2) Ultraviolet radiation (UV) has also been shown to increase the production of ROS in plants. While not fully clarified, the direct interaction with UV absorbing compounds in the cells or effects on the photosynthetic apparatus were suggested as hypothetic mechanisms.

11.3 Antioxidative and photoprotective systems in plant cells

Since excess excitation energy and the formation of ROS is an inescapable feature of oxygen producing photosynthesis, plants have evolved complex defence and regulation systems controlling the formation and action of ROS. These protective mechanisms include the harmless dissipation of excess light as heat, the quenching of ROS in lipid membranes and water-soluble phases by antioxidative compounds and enzymes, and the repair of oxidatively damaged cell components.

Photosystems (mainly photosystem II) quickly and flexibly adjust the light use efficiency to the instantaneous requirements. Such an adjustment becomes manifest as a reduced efficiency after light exposure, often generally called “photoinhibition”. While this effect has been extensively studied, it is not completely clarified (e.g. Niyogi 2000). Most probably, three different processes contribute: Firstly, the pH gradient across the thylakoid membrane seems to trigger immediate changes in membrane conformation, which lead to a decrease in photochemical efficiency. When studied by chlorophyll fluorescence analysis, this component is called pH- (or energy-) dependent fluorescence quenching, which in fact is a form of energy dissipation as heat. It is quickly reversible upon darkening of the leaf. Secondly, another component of decreased photochemical efficiency is relaxing more slowly and seems to be closely related to the xanthophyll cycle, which comprises three carotenoids, violaxanthin (V), antheraxanthin (A), and zeaxanthin (Z). While zeaxanthin, the de-epoxidised form, is involved in energy dissipation, violaxanthin, the epoxidised form, assists in light harvesting. Reversible enzymatic conversion of zeaxanthin via the intermediate antheraxanthin to violaxanthin enables a flexible adjustment of light use efficiency (Demming-Adams 2003). Thirdly, a further mechanism involves longer recovery times and is probably related to the photodegradation of photosystem proteins, which require de-novo synthesis and repair. While the first and second processes may be regarded as “photoprotective” adaptations, the third one rather represents “photodamage” by excess energy or ROS.

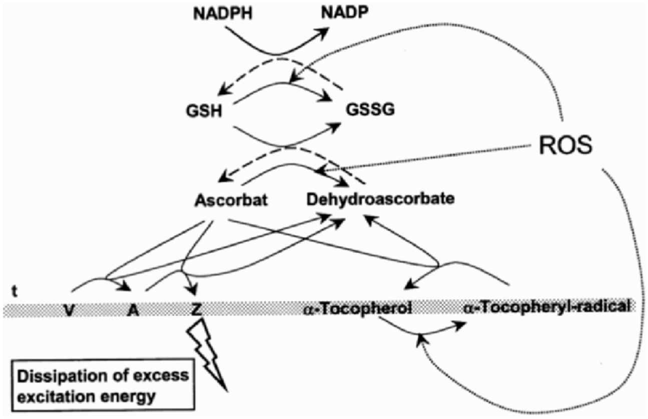

Fig. 11.2. Simplified scheme of some photoprotective and antioxidative systems in chloroplasts. Dashed lines show regeneration (reduction) of oxidised antioxidants, dotted lines show action of reactive oxygen species (ROS). GSH reduced glutathione, GSSG oxidised glutathione. V violaxanthin, A antheraxanthin, Z zeaxanthin, t thylakoid membranes.

Furthermore, because the decrease in quantum efficiency can only decrease photosynthetic electron transport rates to a certain extent under excess excitation energy, other “safety valves” exist in photosynthesis (Asada 1999; Niyogi 2000). These processes, the Mehler-peroxidase reaction and the photorespiration, enable the consumption of electrons by alternative pathways. However, they allow oxygen reduction and, consequently, the formation of ROS which then need to be scavenged. In the Mehler-peroxidase reaction, ROS scavenging is achieved in the glutathione-ascorbate-cycle in the chloroplasts or cytosol. In photorespiration, production and scavenging of ROS is located in specialised compartments (peroxisomes) containing high amounts of catalase, an enzyme which decomposes H_2O_2 to H_2O and O_2.

In the lipid phase of the thylakoid membranes, carotenoids and tocopherols are the most effective defence systems. Besides their role in the quenching of excess energy, carotenoids, such as β-carotene or lutein, may also de-exite singlet oxygen and chemically scavenge ROS. α-Tocopherol is abundant in green plant tissues, and mainly located in thylakoids and chloroplast envelopes. It is a powerful antioxidant acting as a chemical scavenger of ROS and a quencher of singlet oxygen. Furthermore, it is able to scavenge lipid peroxides (oxidation products of membrane lipids) thus protecting membranes from damage (Munné-Bosch and Alegre 2002). α-Tocopherol is regenerated by ascorbate, which links the membrane-bound to the water soluble antioxidant defence systems (Fig. 11.2).

Ascorbic acid is quantitatively the predominant water soluble antioxidant in plant cells. It is a multifacetted molecule which acts as a chemical scavenger of ROS, as a substrate in the enzymatic removal of H_2O_2, and is required for the conversions of the xanthophyll cycle and the regeneration of tocopherol (Smirnoff 2000). When oxidised by ROS, short-lived monodehydroascorbate is formed, which can be regenerated directly or disproportionates into dehydroascorbate. The latter is regenerated by reduced glutathione in an enzymatic cycle (Foyer and Noctor 1998).

The glutathione redox system (the redox pair reduced/oxidised glutathione) is not only required for the maintenance of ascorbate redox state, but also involved in a multitude of protective and regulative actions within the cells (Tausz 2001).

11.4 Factors causing photo-oxidative stress at the timberline

A number of environmental factors typical of the alpine timberline can cause (photo-)oxidative stress in plants, and a number of observations corroborate the importance of this mechanism for alpine plant life in general and tree life in particular.

(1) The frequent combination of high solar radiation with low temperatures (also called “photo-chilling”) can induce photoinhibition and high amounts of ROS formation (Baczek-Kwinta et al. 2005; Allen and Ort 2001). At low temperatures, the Calvin cycle is inhibited, which leads to excess absorbed energy and over-reduction of the electron transport chains. Resistance to photoinhibitory damage under low temperatures conditions (due to ROS) is also crucial for high alpine plants (e. g. Streb et al. 1998) and trees at the timberline. At high elevations, spring time or the transition from autumn to winter are the potentially most stressful times of the season in this respect. Photo-oxidative stress and photoinhibition related to photo-chilling (high light and low temperature exposure) have been observed in a variety of timberline tree species and ecosystems, e. g. in North America (*Picea engelmannii* and *Abies lasiocarpa*, Germino and Smith 1999)), Europe (e. g. *Picea abies*, *Pinus mugo*, Robakowski 2005), Australia (e. g. *Eucalyptus pauciflora*, Blennow et al. 1998), or subtropical (sub)alpine ecosystems (e. g. *Picea morrisonicola* in Taiwan, Weng et al. 2005), to name but a few.

(2) High ozone concentrations at higher elevations in the Alps may contribute to overall high oxidative stress. Ozone is a secondary air pollutant produced from precursors (mainly nitrogen oxides, hydrocarbons etc.) under UV influence. Timberlines are generally remote from pollution sources, but long-distance transport of polluted air masses promotes the formation of ozone and leads to chronically high concentrations at high elevations (Herman et al. 2001). Near the Alpine timberlines, ozone exposure indices such as the AOT40 ("accumulated dose over a threshold of 40 nl l^{-1}") regularly exceed the provisional critical values for risk of damage to forest trees. Although recent research suggests that most timberline tree species are more resistant to such concentrations than the provisional critical values suggest, a significant contribution of O_3 to the overall "high elevation stress" is very likely.

(3) Due to its energy, UV-B (280-320 nm) has a high potential for causing biological damage (Mackerness 2000). UV radiation (as other radiation qualities) tends to rise with increasing elevation. The proportion of UV-B in total solar radiation increases in a thinner, clear, and unpolluted mountain atmosphere. Although UV-B effects on plants are much less well studied than on mammals, it seems clear that it leads primarily to oxidative stress in plants (Mackerness 2000). Whether ROS formation in UV-B stressed plants originates in the chloroplasts due to damages in the thylakoid membranes, or whether other interactions with cellular components are the main source, is not decided (Mackerness 2000). It must be noted that plants grown at high elevations seem well protected, because they possess effective UV-B screening compounds in outer cell layers (Turunen and Latola 2005). Hence, in contrast to controlled environment experiments, field studies often failed to establish clear UV-B effects on plants, in particular in the short term (Turunen and Latola 2005).

(4) A number of other environmental factors can cause oxidative stress in plants. Drought, heat, wounding, frost, and anoxia due to water logging have all been associated with enhanced ROS production and oxidative stress in plants. Their importance at alpine timberlines may vary, but some of them are possibly significant.

11.5 Antioxidative and photoprotective responses of trees at high elevations

In the beginning of the nineties of the last century, it has been observed that trees at higher elevated plots accumulate higher concentrations of protective substances – antioxidants and photoprotective carotenoids - in leaf tissues (Fig. 11.3). Spruce needles from trees at timberline plots often contain higher concentrations of ascorbate, glutathione, tocopherol, or carotenoids (Polle et al. 1992; Polle and Rennenberg 1992; Tausz et al. 1998; Table 11.1), potentially conferring better protection from photo-oxidative stress. Chlorophyll concentrations, on the other hand, follow a reverse gradient (Polle et al. 1992; Tausz et al. 1998; see Table 11.1). Lower chlorophyll concentrations can be a consequence of photo-oxidative damage to green tissues, but less chlorophyll also reduces energy absorption and, hence, the risk of photo-oxidative stress. In this latter view, lower chlorophyll concentrations would be an adaptation to the higher risk of photo-oxidative stress rather than a damage symptom. Similar results as for spruce were obtained in larch needles in Northern and Southern Calcareous Alps (Hecke et al. 2003): Needles collected at near timberline plots contained more glutathione and protective carotenoids, but less chlorophyll than needles from valley plots.

Grill et al. (1988) showed that the accumulation of low-molecular weight thiols (mainly glutathione) at high elevations occurred irrespective of the provenance of the (spruce) trees used, suggesting that the environmental challenge dominated over genotypic determination. This study investigated 20-years old spruce trees of high- and low-elevation provenance grown in common plantation trials at high and low elevation. Other studies could not corroborate this finding: Polle et al. (1999) found that young spruce clones did not consistently increase antioxidants when planted at high elevations. The authors concluded that different genotypes may have different abilities to acclimate to the high elevation conditions, but an alternatively explanation would be that the acclimation of the protection systems requires longer exposure times. A previous study on spruce genotypes revealed that although there was a genotypic component to thiol (glutathione) contents in spruce needles, genotype differences disappeared after growing the trees at a certain elevation for some years (Guttenberger et al. 1992).

Work on herbaceous high Alpine species underlined the importance of antioxidative and photoprotective defence systems in coping with high elevation stress (Wildi and Lütz 1996; Table 11.1). In most of the investigated species antioxidants increased at higher elevated sites, although it became clear that different species may employ different antioxidants to a different extent, and not all species showed increased total antioxidant levels. Contrary to most trees growing at the timberline, many specialised high Alpine species did not show decreased chlorophyll contents with increasing elevation, which is perhaps indicative of better protection against excess excitation energy absorbed by chlorophyll (Table 11.1).

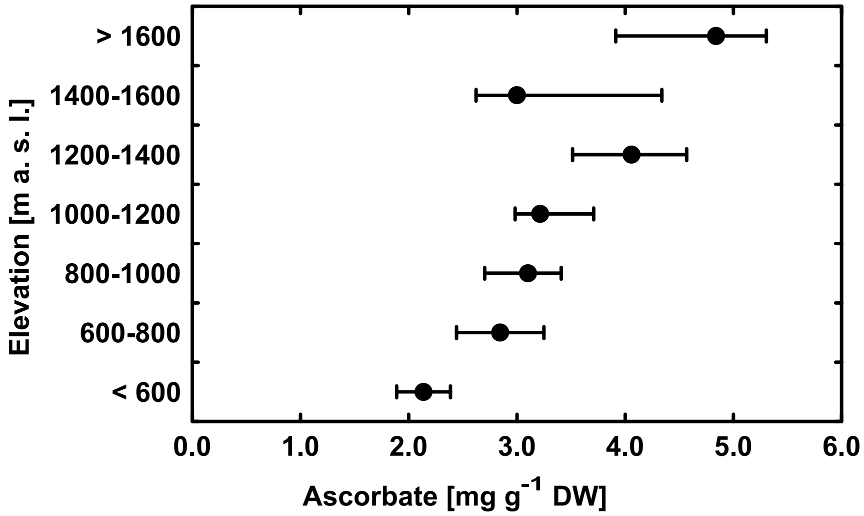

Fig. 11.3. Ascorbate concentrations in 1-year-old needles of Norway spruce trees from altitudinal gradients in the Austrian Alps. (Modified after Tausz et al. 1997.) DW needle dry weight. Medians and quartile ranges.

Although these data seem to corroborate a general requirement of high alpine plants for high antioxidative protection, there are notable exceptions inasmuch as some plant species did not show enhanced antioxidant level at higher elevated sites (Wildi and Lütz 1996; Table 11.1). As discussed before, there is no single mechanism for withstanding photo-oxidative stress. For example, a sustained high capacity for electron consumption in carbon assimilation or photorespiration may make high levels of the antioxidants listed in Table 11.1 redundant. Findings that co-occurring high alpine species can use very different sets of protective mechanisms support this view. Streb et al. (1998), e.g., demonstrated that out of three investigated high Alpine species only two (*Soldanella alpina* and *Homogyne alpina*) had a high capacity for antioxidative protection relative to lowland plants, but not the third one (*Ranunculus glacialis*). The authors concluded that *R. glacialis* rather relied on photorespiration as an alternative electron sink to avoid increased ROS production. Williams et al. (2003) found correspondingly, that out of six co-occurring Tasmanian alpine heath species, one maintained a high capacity for electron transport and hence had a low requirement for additional photoprotective responses, such as increased zeaxanthin formation.

Table 11.1. Percent change of foliar content of total chlorophyll and ascorbic acid of some Alpine timberline trees and high Alpine herbaceous species per 1000 m difference in elevation (lower elevation value = 100 %). Chl chlorophyll.

Variable	Species	Change	Elevation range	Ref
Total Chl	*Picea abies;* mature trees	- 31 %	600-1600	1)
	P. abies; mature trees	- 41 to -60 %*	870-1700	6)
	P. abies; mature trees	-57 %	800 - 1750	4)
	P. abies; 3-years-old clones	-57 to -67 %	800 - 1750	4)
	Larix decidua; mature trees	- 3 to -19 %	1000 - 2000	3)
	Soldanella pusilla	-16 %	1000 - 2000	5)
	Homogyne alpina	+1 %	1000 - 2000	5)
	Poa laxa	+7 %	2000 - 3000	5)
	Tanacetum alpinum	+2 %	2000 - 3000	5)
	Ranunculus glacialis	± 0 %	2000 - 3000	5)
	Taraxacum alpinum	+38 %	1000 - 2000	5)
	Taraxacum alpinum	-26 %	2000 - 3000	5)
	Carex curvula	-18 to -24 %	2000 - 3000	5)
	Geum reptans	-11 to -19 %	2000 - 3000	5)
	Dryas octopetala	-65 %	450 - 1000	5)
	Dryas octopetala	+15 %	1000 - 2000	5)
Ascorbic acid	*Picea abie ;* mature trees	+ 178 %	600 - 1600	1)
	P. abies; mature trees	+ 23 to + 40%	870 - 1700	2)
	P. abies; mature trees	+ 9 %	800 - 1750	4)
	P. abies; 3-years-old clones	± 0 to +72 %	800 - 1750	4)
	Larix decidua; mature trees	- 28 to + 167 %	1000 - 2000	3)
	Soldanella pusilla	+ 24 %	1000 - 2000	5)
	Homogyne alpina	+ 950 %	1000 - 2000	5)
	Poa laxa	+ 213 %	2000 - 3000	5)
	Tanacetum alpinum	+ 488 %	2000 - 3000	5)
	Ranunculus glacialis	+ 116 %	2000 - 3000	5)
	Taraxacum alpinum	+24 %	1000 - 2000	5)
	Taraxacum alpinum	- 53 %	2000 - 3000	5)
	Carex curvula	+977 to +1110 %	2000 - 3000	5)
	Geum reptans	+589 to +654 %	2000 - 3000	5)
	Dryas octopetala	+15 %	450 - 1000	5)
	Dryas octopetala	-90 %	1000 - 2000	5)

1) Tausz et al. 1997; 2) Polle and Rennenberg 1992; 3) Hecke et al. 2003; 4) Polle et al. 1999; 5) Wildi and Lütz 1996; 6) Polle et al. 1992.

Table 11.1. Continued.

Variable	Species	Change	Elevation range	Ref
Tocopherol	*Larix decidua*; mature trees	- 10 to + 33 %	1000 - 2000	3)
	Soldanella pusilla	+ 258 %	1000 - 2000	5)
	Homogyne alpina	+ 120 %	1000 - 2000	5)
	Poa laxa	- 76 %	2000 - 3000	5)
	Tanacetum alpinum	± 0 %	2000 - 3000	5)
	Ranunculus glacialis	+ 263 %	2000 - 3000	5)
	Taraxacum alpinum	-56 %	1000 - 2000	5)
	Taraxacum alpinum	-19 %	2000 - 3000	5)
	Carex curvula	-46 to -54 %	2000 - 3000	5)
	Geum reptans	-8 to +8 %	2000 - 3000	5)
	Dryas octopetala	-121 %	450 – 1000	5)
	Dryas octopetala	-36 %	1000 - 2000	5)
Glutathione	Picea abies; mature trees	+ 120 %	600-1600	1)
	P. abies; mature trees	+ 25 to + 85 %	870-1700	2)
	P. abies; 20-years-old trees	+ 43 to + 84 %	400 - 1700	7)
	P. abies; mature trees	+26 %	800 - 1750	4)
	P. abies; 3-years-old clones	± 0 to -24 %	800 - 1750	4)
	Larix decidua; mature trees	+ 96 to + 100 %	1000 - 2000	3)
	Soldanella pusilla	+ 204 %	1000 - 2000	5)
	Homogyne alpina	+ 520 %	1000 - 2000	5)
	Plantago major	+ 22 %	1600 - 2600	8)
	Poa laxa	+ 220 %	2000 - 3000	5)
	Tanacetum alpinum	+ 10 %	2000 - 3000	5)
	Ranunculus glacialis	+ 7 %	2000 - 3000	5)
	Taraxacum alpinum	+630 %	1000 - 2000	5)
	Taraxacum alpinum	-92 %	2000 - 3000	5)
	Carex curvula	-49 to -68 %	2000 - 3000	5)
	Geum reptans	-25 %	2000 - 3000	5)
	Dryas octopetala	±0 %	450 – 1000	5)
	Dryas octopetala	+600 %	1000 - 2000	5)

1) Tausz et al. 1997; 2) Polle and Rennenberg 1992; 3) Hecke et al. 2003; 4) Polle et al. 1999; 5) Wildi and Lütz 1996; 6) Polle et al. 1992; 7) Grill et al. 1988; 8) Ren et al. 1999.

When comparing highly specialised alpine species to timberline trees it must be noted that trees quite obviously operate at the survival limit, not only of their species, but of the life-form tree in general. The question whether high antioxidant concentrations are a marker of adaptation or acclimation or a marker of stress and damage must be addressed. Data derived from experiments with slowly progressing stress impact (drought exposure) suggest that transient changes in redox states precede acclimatory increases in antioxidant concentrations, but that a more pronounced oxidation of antioxidant pools indicates incipient breakdown of the system (Šircelj et al. 2005). Only few analyses of this type have been done at timberline systems (see some examples below).

The data compiled in Table 11.1 combine measurements made during the main vegetation period, mainly taken in late summer. Investigations of antioxidative defence compounds during winter, which may be more stressful for timberline trees, are less frequently reported. Generally, antioxidant contents are higher during winter, which may be related to frost hardening (Esterbauer and Grill 1978; Polle and Rennenberg 1992; Stecher et al. 1999). It was shown for *Pinus cembra* and *Picea abies* that the loss of photosynthetic capacity during winter was not related to an oxidation of ascorbate and glutathione pools (Stecher et al. 1999). It was concluded that winter photoinhibition was not caused by increased action of ROS and oxidative damage to the photosystems, but rather a consequence of photoprotective changes such as increased zeaxanthin formation. It seems that important European timberline species – *Pinus cembra* and *Pinus mugo* - are well-protected against photodamage even during winter (Lehner and Lütz 2003) and well equipped to start effective photosynthesis quickly under favourable conditions.

11.6 To which extent do photo-oxidative stress and photoinhibition limit tree growth at the timberline?

While it can be concluded from the results discussed in the previous sections that photo-oxidative stress and photoinhibition play important roles under environmental conditions at alpine timberlines, their overall quantitative effects on tree competitiveness and survival is largely unknown. Photoinhibition in its widest definition is a light-induced decrease in photosynthetic carbon gain. However, only slow relaxing photoinhibition (which is possibly due to degradation of thylakoid proteins) is likely to affect the carbon balance of trees directly. Faster relaxing components of photoinhibition merely dissipate excess excitation energy not usable for carbon fixation and thereby protect leaves from excess light. Surprisingly few attempts have been made to model the effect of slowly recovering photoinhibition on C-gain directly; some recent examples include maize (Zhu et al. 2004) and the evergreen oak *Quercus coccifera* (Werner et al. 2001). These models predicted decreases in C-gain between 6 and 30 % due to slowly relaxing photoinhibition, and we may assume that the values are higher for trees at the timberline.

There is some doubt whether the photosynthetic processes at the leaf level can explain timberline formation from a global perspective at all. Körner (2003) mentioned "phototoxic effects" as part of the "stress hypothesis" – one hypothesis put forward to explain timberline formation – but he argued a sink limitation hypothesis, i.e. a limitation by the lack of "possibilites for investment" of resources as a more general explanation for timberline formation. It is, however, accepted that stress impact and phototoxic effects will play a role in the local fine-tuning of the timberline positions or in locally important competition between species.

At present, it seems safe to accept that photo-oxidative stress has a role in limiting the establishment and distribution of tree seedlings at certain timberline ecotones or beyond the existing closed forest. A number of studies not only showed low temperature related photoinhibition in tree species, but also related it to seedling establishment and growth in the field (Ball et al. 1991; Germino and Smith 1999). In particular, seedling establishment was often restricted to more shaded locations, where strong photoinhibition was avoided. Shadecloth shelters were shown to alleviate growth limitations due to low temperature photoinhibition during the establishment of tree seedlings (Close et al. 2002). A modelling exercise for the North American *Abies lasiocarpa* and *Picea engelmannii* suggested that the daily C gain of seedlings at the timberline was higher on cloudy days (Johnson et al. 2004), when photoinhibition would be avoided. However, for saplings of *Picea abies* and *Pinus cembra*, major timberline species in the Alps, the growth light regime had no effect on their resistance to high light exposure and photoinhibition was not stronger at 5 °C than at 15 °C (Gamper et al. 2000). This underlines that there are important differences between species and ecosystems (Germino and Smith 1999).

Hence, we may not expect a general answer to these open questions. The defence mechanisms are a complex network of different pathways, which may have different relative importance in different plants. The biochemical defence mechanisms against photo-oxidative stress discussed in this chapter come on top of structural and morphological adaptations to avoid high light stress – e.g. specialised hairs and leaf surfaces, leaf angles enabling avoidance of maximum light impact etc. Hence, the relative importance of biochemical defence systems in limiting tree growth and determining timberline positions must probably be assessed on a case by case basis and will most likely be fairly different between different species and ecosystems.

References

Asada K (1999) The water-water cycle in chloroplasts: scavenging of active oxygen and dissipation of excess photons. Annual Review of Plant Physiology and Plant Molecular Biology 50: 601-639

Baczek-Kwinta R, Niewiadomska E, Miszalski Z (2005) Physiological role of reactive oxygen species in chill-sensitive plants. Phyton 45: 25-37

Ball MC, Hodges VS, Laughlin GP (1991) Cold-induced photoinhibition limits regeneration of snow gum at tree-line. Functional Ecology 5: 663-668

Blennow K, Lang ARG, Dunne P, Ball MC (1998) Cold-induced photoinhibition and growth of seedling snow gum (*Eucalyptus pauciflora*) under differing temperature and radiation regimes in fragmented forests. Plant, Cell and Environment. 21: 407-416

Close DC, Beadle CL, Holz GK, Brown PH (20029 Effect of shadecloth tree shelters on cold-induced photoinhibition, foliar anthocyanin and growth of *Eucalyptus globulus* and *E. nitens* seedlings during establishment. Australian Journal of Botany 50: 15-20

Demmig-Adams B (2003) Linking the xanthophyll cycle with thermal energy dissipation. Photosynthesis Research 76: 73-80.

Elstner EF, Oßwald W (1994) Mechanisms of oxygen activation during plant stress. Proceedings of the Royal Society of Edinburgh B Biology 102: 131-154

Esterbauer H, Grill D (1978) Seasonal variation of glutathione and glutathione reductase in needles of *Picea abies*. Plant Physiology 61:119-121

Foyer CH, Noctor G (2000) Oxygen processing in photosynthesis: regulation and signalling. New Phytologist 146: 359-388

Gamper R, Mayr S, Bauer H (2000) Similar susceptibility to excess irradiance in sun and shade acclimated saplings of Norway spruce [*Picea abies* (L.) Karst.] and stone pine (*Pinus cembra* L.). Photosynthetica 38: 373-378

Germino MJ, Smith WK (1999) Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. Plant, Cell and Environment 22: 407-415

Grill D, Pfeifhofer H, Tschulik A, Hellig K, Holzer K (1988) Thiol content of spruce needles at forest limits. Oecologia 76: 294-297

Guttenberger H, Bermadinger E, Grill D, Holzer K (1992) Water-soluble thiols in spruce seedlings from provenances of different sea levels. Phyton 31: 217-226

Hecke K, Tausz M, Gigele T, Havranek WM, Anfodillo T, Grill D (2003) Foliar antioxidants and protective pigments in *Larix decidua* Mill. from contrasting elevations in the northern and southern Tyrolean Limestone Alps. Forstwissenschaftliches Centralblatt 122: 368-375

Herman F, Smidt S, Huber S, Englisch M, Knoflacher M (2001) Evaluation of pollution-related stress factors for forest ecosystems in central Europe. Environmental Science and Pollution Research 8: 231-242

Johnson DM, Germino MJ, Smith WK (2004) Abiotic factors limiting photosynthesis in *Abies lasiocarpa* and *Picea engelmannii* seedlings below and above the alpine timberline. Tree Physiology 24: 377-386

Körner Ch (2003) Alpine plant life: functional plant ecology of high mountain ecosystems, 2nd edn. Springer, Berlin

Lehner G, Lütz C (2003) Photosynthetic functions of cembran pines and dwarf pines during winter at timberline as regulated by different temperatures, snowcover and light. Journal of Plant Physiology. 160: 153-166

Mackerness SAH (2000) Plant responses to ultraviolet-B (UV-B: 280-320 nm) stress: What are the key regulators? Invited review. Plant Growth Regulation 32: 27-39

Munné-Bosch S, Alegre L (2002) The function of tocopherols and tocotrienols in plants. Critical Reviews in Plant Sciences 21: 31–57

Niyogi KK (2000) Safety valves for photosynthesis. Current Opinion in Plant Biology 3: 455-460

Polle A, Rennenberg H (1992) Field studies on Norway spruce trees at high altitudes. II. Defence systems against oxidative stress in needles. New Phytologist 121: 635-642

Polle A, Mössnang M, von Schönborn A, Sladkovic R, Rennenberg H (1992) Field studies on Norway spruce trees at high altitudes. I. Mineral, pigment and soluble protein contents of needles as affected by climate and pollution. New Phytologist 121: 89-99

Polle A, Baumbusch LO, Oschinski C, Eiblmeier M, Kuhlenkamp V, Vollrath B, Scholz F, Rennenberg H (1999) Growth and protection against oxidative stress in young clones and mature spruce trees (*Picea abies* L.) at high altitudes. Oecologia 121: 149-156

Ren H-X, Wang Z-L, Chen X, Zhu Y-L (1999) Antioxidative responses to different altitudes in *Plantago major*. Experimental and Environmental Botany 42: 51-59

Robakowski P (2005) Susceptibility to low-temperature photoinhibition in three conifers differing in successional status. Tree Physiology 25: 1151-1160

Šircelj H, Tausz M, Grill D, Batič F (2005) Biochemical responses of two apple cultivars subjected to progressive drought. Journal of Plant Physiology 162: 1308-1318

Smirnoff N (2000) Ascorbic acid: metabolism and functions of a multi-facetted molecule. Current Opinion in Plant Biology 3: 229–235

Stecher G, Schwienbacher F, Mayr S, Bauer H (1999) Effects of winter-stress on photosynthesis and antioxidants of exposed and shaded needles of *Picea abies* (L.) Karst. and *Pinus cembra* L. Phyton 39: 205-211

Streb P, Shang W, Feierabend J, Bligny R (1998) Divergent strategies of photoprotection in high-mountain plants. Planta 207: 313-324

Tausz M (2001) The role of glutathione in plant reaction and adaptation to natural stresses. In: Grill D, Tausz M, DeKok LJ (eds) Significance of glutathione in plant adaptation to the environment. Handbook Series of Plant Ecophysiology, vol 2. Kluwer Academic Publishers, Amsterdam, pp 101-122

Tausz M, Grill D, Jiménez MS, Morales D (1997) A physiological comparison between environmental effects on Canary pine in Tenerife and Norway spruce in Austria. In: Mohren F, Kramer K, Sabate S (eds) Impacts of global change on tree physiology and forest ecosystems. Kluwer Academic Publishers, Amsterdam, pp 103-110

Turunen M, Latola K (2005) UV-B radiation and acclimation in timberline plants. Environmental Pollution 137: 390-403

Weng JH, Liao TS, Sun KH, Chung JC, Lin CP, Chu CH (2005) Seasonal variations in photosynthesis of *Picea morrisonicola* growing in the subalpine region of subtropical Taiwan. Tree Physiology 25: 973-979

Werner C, Ryel RJ, Correia O, Beyschlag W (2001) Effects of photoinhibition on whole-plant carbon gain assessed with a photosynthesis model. Plant, Cell and Environment 24: 27-40

Wildi B, Lütz C (1996) Antioxidant composition of selected high alpine plant species from different altitudes. Plant, Cell and Environment 19: 138-146

Williams EL, Hovenden MJ, Close DC (2003) Strategies of light energy utilisation, dissipation and attenuation in six co-occurring alpine heath species in Tasmania. Functional Plant Biology 30: 1205-1218

Zhu XG, Portis AR, Long SP (2004) Would transformation of C_3 crop plants with foreign Rubisco increase productivity? A computational analysis extrapolating from kinetic properties to canopy photosynthesis. Plant Cell and Environment. 27:155-165

12 Global Change at the Upper Timberline

Gerhard Wieser

Institut für Naturgefahren und Waldgrenzregionen, BFW, Innsbruck

12.1 Introduction

Forests in temperate mountain systems cover approximately 6 % of the area of Europe. Timberline associated forest ecosystems are of particular interest because they are expected to undergo significant changes within the next century (cf. Walther et al. 2005). Compared to always occurring natural changes in conditions for tree and plant life which are commonly rather slow, current human induced global changes by contrast are more rapid. In this chapter the discussion will be on human impacts on tree life at the alpine timberline including changes in land use and management, changes in the chemical composition of the lower atmosphere, climate warming, and an increasing ultraviolet-B radiation.

12.2 Land use and management

Land use in the central European Alps is as old as the presence of human activities (Conrad 1940; Damm 1998) which was found up to 3000 m above sea level (Bortenschlager and Oeggl 2000) where shepherds presently still have their pastures. Pasturing has influenced the timberline ecotone for at least 7000 years (Patzelt 1996). Nearly all the moderate slopes that were easily accessible were often deforested (Leidlmair 1983; Holtmeier 1973) due to land use for seasonal pasturing of domestic animals and thus having significantly lowered the natural treeline 150 to 300 m below the postglacial level of the climatic treeline (Holtmeier 1986;

G. Wieser and M. Tausz (eds.), Trees at their Upper Limit, 197–217.

1994). In many regions timber was also used for mining, firewood, and construction wood (Stern 1966; Mayer 1970).

Nevertheless, due to sustainable management these forms of land use only exceptionally lead to erosions (Körner 2003). However, deforestation, uncontrolled grazing, stocking beyond the carrying capacity, too heavy animals, and abandonment may affect soils and may force erosion (Stiny 1910; Schiechtl 1954; Aulitzky 1994; Ammer et al. 1996). Land use also influenced the composition and the structure of high-elevation forests. Prolonged grazing caused subalpine forests to become over mature. *Pinus cembra* is less tolerant to grazing and trampling as compared to *Larix decidua* (Holtmeier 2003). Trampling causes an uncovering of the mineral soil and thus favouring seedling establishment for *Larix*, while *Pinus*, which is spread by the European nutcracker (*Nucifraga caryocatactes*) favours pastures.

Moreover, rather severe albeit more localized forms of anthropogenic impacts in recent times are the construction of ski runs (Cernusca 1977), artificial snow (Cernusca et al. 1990), transport routes, summer tourism, and their infrastructure. New forms of recreation activities like skiing and mountain biking outside official tracks are also described to have adverse effects on soils and plant cover, especially above the forest limit (Cernusca 1978). However, most of these intensive types of land use by humans due to recreation activities are in general small in area as compared to agricultural land use. But, on the other hand such man made impacts often affect a rather sensitive terrain such as steep slopes and hence starting zones of avalanches and land slides (Holtmeier 1973; Aulitzky 1994, 1996). Reafforestation may help in some places (Kronfuss and Havranek 1999) but the stable naturally developed root-mycorrhiza-soil systems can not easily be recovered (Göbl 1965; Keller 1997) due to changes in soil nutrient conditions and a rather low self-repair, and often requires plant disease-control arrangements (Donaubauer 1980).

12.3 Altered atmospheric environment

Gases such as ozone (O_3), sulphur dioxide (SO_2) and nitrogen oxides (NO_x) have always been natural constituents of the atmosphere. However, during the last century the composition of the lower troposphere over Europe has drastically changed and O_3 concentrations have at least doubled during the last 100 years (Volz and Kley 1988; Marenco et al. 1994) while SO_2 and NO_x concentrations are close to background levels (Smidt and Gabler 1994).

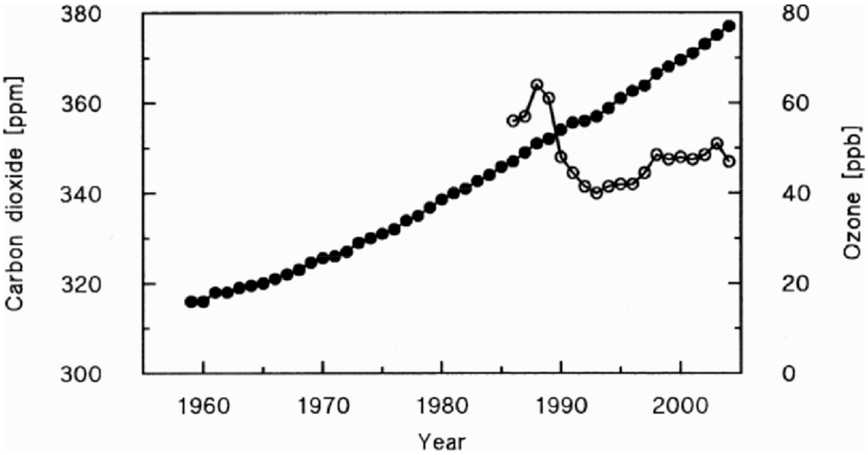

Fig. 12.1. Annual average atmospheric CO_2 concentration at Manua Loa, Hawaii (solid circles; source: Keeling, Wholf and Carbon Dioxide Research Group SIO, University of California, Aug 2005; http://www.cdiac.esd.ornl.gov) and ambient ozone concentration at timberline in the central Austrian Alps (open circles; source: Amt der Tiroler Landesregierung 2005).

Nowadays high elevation forest ecosystems in the European Alps can experience O_3 episodes above 100 to 120 ppb (Schneider et al. 1996) with annual mean values ranging from 40 to 50 ppb (Fig. 12.1; Bianco and Dalstein 1999; Smidt 1998; Amt der Tiroler Landesregierung 2005). Especially in the southern parts of the European Alps air pollutant emissions from neighbouring urban and industrial districts (Dalstein et al. 2002) and climatic conditions as well as orographical features favour the formation of photochemical smog and the occurrence of high O_3 concentrations (Vecci and Valli 1999).

12.3.1 Effects of elevated ozone

Results of O_3 fumigation experiments carried out in the in the central Austrian Alps clearly showed that even two-fold ambient O_3 concentrations did neither cause any visible injury such as chloroses, chlorotic mottling, or necrotic spots, nor affected specific leaf area and 100-needle dry weight (Wieser and Havrenek 2001) in current- and one-year old needles of *Picea abies* (Havranek et al 1989) and *Pinus cembra* (Wieser et al. 2006), as well as in *Larix decidua* needles (Volgger 1995).

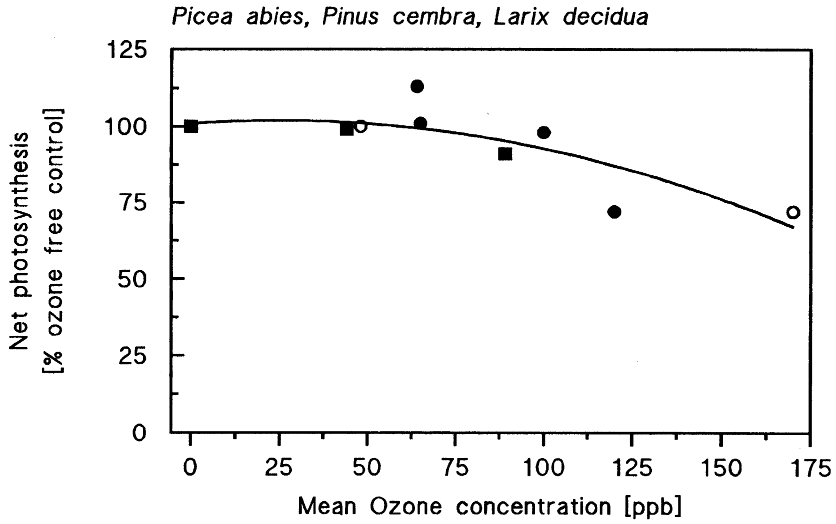

Fig. 12.2. Net photosynthesis of *Picea abies* (●), *Pinus cembra* (■), and *Larix decidua* (○) twigs after exposure to different O_3 treatments in relation to mean O_3 concentration during one fumigation period. Measurements were conducted *in situ* at Mt. Patscherkofel (Klimahaus), Austria 1950 m a.s.l. at controlled conditions (light saturation, 21 °C needle temperature, 10 Pa kPa^{-1} leaf to air water vapour pressure difference, 350 ppm CO_2). Mean ambient O_3 concentrations during the fumigation periods (8 to 13 weeks) were 45-65 ppb. Points were fit by polynomial regression: $y = (-0.0017 *x + 0.085) * x + 100$; $r^2 = 0.68$. (Redrawn after data from Havranek et al. 1989; Volgger 1995; and Wieser et al. 2006.)

After fumigation throughout one growing season with mean O_3 concentrations ranging from zero to 100 ppb no distinct treatment effects were detectable in net photosynthesis (Fig. 12.2), night-time dark respiration, and the optimum photochemical efficiency of photosystem II. Mean O_3 concentrations above 100 ppb however, induced a significant decline in net photosynthesis by 25-30 % (Fig. 12.2).

The only sign of O_3 induced changes in the composition of photosynthetic pigments and antioxidants was a significant increase in the deepoxidation state of the xanthophylls cycle and a decrease in the amount of oxidised glutathione in one year-old *Pinus cembra* needles under the presence of ambient O_3 (Wieser et al. 2001, 2005). Such changes in the redox state of glutathione are supposed to be an indicator for early stages of hidden O_3 injury as shown for O_3 sensitive field grown *Pinus ponderosa* trees (Tausz et al. 1999) and have generally been suggested as early responses in plant stress reactions (Tausz et al. 2004). However, this response must be regarded as marginal, because two-fold ambient O_3 exposure has no effects on photosynthetic pigments and antioxidant contents.

Although in the central Austrian Alps evidence of O_3 injury on forest trees is lacking (Matyssek et al. 1997) one-year old needles of *Pinus cembra* trees in declining stands in the southern French Alps showed symptoms of yellowing and defoliation (Bianco and Dalstein 1999; Dalstein et al. 2002). By means of microscopic methods these observed symptoms could clearly be attributed to visible O_3 injury (Vollenweider et al. 2003). As O_3 effects depend on the amount of O_3 taken up by the needles via the stomata (Wieser and Havranek 1993; Matyssek et al. 1997) differences in O_3 uptake seem to be the key factor for explaining the observed decline in *Pinus cembra* in alpine regions in southern France, as there is evidence that stomatal conductance was significantly higher in needles of declining trees as compared to healthy trees (Dalstein et al. 2002). Thus, the action of O_3 must always be evaluated in concert with other environmental impacts which all together determine the tree's sensitivity to stress.

12.3.2 Effects of elevated CO_2

The rise in atmospheric CO_2 concentration is another global phenomenon (Fig. 12.1) and CO_2 concentrations are currently rising at a rate of 1 - 2 ppm year^{-1} (Keeling et al. 1995). Trees within the timberline ecotone may be particularly sensitive to increasing CO_2 because they grow in an environment with a low partial pressure of CO_2 (see Chap. 2). Results of a three-year free air CO_2 enrichment (ambient plus 73 to 81 %) at the alpine timberline in Switzerland (Stillberg, Davos) at 2180 m a.s.l. showed that light saturated net photosynthesis in 30-year-old *Larix decidua* and *Pinus uncinata* trees was significantly higher when grown and measured under elevated CO_2 as compared to ambient CO_2 control trees (Hättenschwiler et al. 2002; Handa et al. 2005; Fig. 12.3). However, the enhancement of photosynthesis under elevated CO_2 tended to decline with increasing exposure duration (Fig. 12.3). Furthermore, when trees grown under elevated CO_2 were measured under ambient CO_2 concentration and *vice versa* there was no significant evidence for a photosynthetic down regulation in both tree species (Handa et al. 2005), a behaviour of gas exchange which is typically for field grown trees exposed to elevated CO_2 (Curtis 1996).

Both species also increased their total non structural carbohydrate content by 7 to 37 % by increasing their starch fraction when grown under elevated CO_2, and this contributes to a decline in the specific leaf area as needles became heavier (Hättenschwiler et al. 2002; Handa et al. 2005).

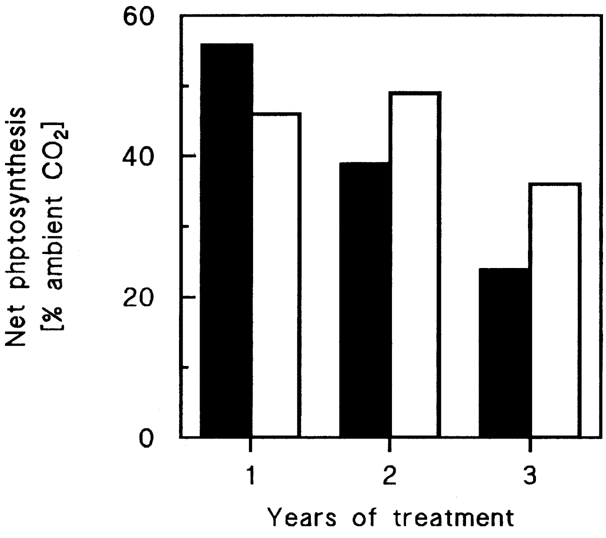

Fig. 12.3. Photosynthetic enhancement in % of ambient CO_2 in *Pinus uncinata* (solid bars) and *Larix decidua* (open bars) trees exposed to elevated CO_2 (566-582 ppm) in relation to exposure duration. Measurements were made *in situ* at the treatment CO_2 concentration where trees were growing at Stillberg, Switzerland 2180m a.s.l. (Redrawn after data from Hättenschwiler et al. 2002; and Handa et al. 2005.)

This built-up of carbohydrates strongly suggests that trees at the treeline are not limited by the supply of photosynthetic assimilates but rather by the rate at which glucose can be utilized (Grace et al. 2002). In addition, there was no response of shoot growth to elevated CO_2 in *Pinus uncinata* while in *Larix decidua* CO_2 enhancement caused a significant stimulation in lateral shoot growth of up to 50 % (Handa et al. 2005). These observed differences within species in growth response may be due to contrasting leaf life strategies in deciduous as compared to evergreen conifers (Cornelissen et al. 1999).

It is difficult to assess whether the higher observed growth enhancement in *Larix* as compared to *Pinus* persists under field conditions in the long term in parallel with the rising atmospheric CO_2 concentrations over the last 150 years, because there is evidence that the size and mass increment of both species did not differ over the last 23 years (Bernoulli and Körner 1999). Furthermore, three years of CO_2 enrichment in the timberline ecotone, where short growing seasons alternate with long resting periods, might be too short to draw unambiguous conclusions to long-term responses (Saxe et al. 1998; Norby et al.1999) as there is evidence that CO_2 effects will decline over time due to age related stand dynamics in competition to above and below ground resources (Hättenschwiler et al. 1997).

On the other hand, tree-ring widths of conifers within the timberline ecotone tended to increase during the last 150 years (Nicolussi et al. 1995; Rolland et al. 1998; Paulsen et al. 2002) and both, increased atmospheric CO_2 concentration (Kienast and Luxmore 1988; Fig. 12.1), as well as increased temperature (Innes 1991; Graumlich 1991; Wuebbles et al. 1999; Grace et al. 2002) have been suggested as possible causes for the observed increase in growth. Nicolussi et al. (1995) however, used selected periods of equal mean summer temperatures to minimize these uncertainties and concluded that atmospheric CO_2 enrichment (Fig. 12.1) appears to be the most plausible explanation for the observed increase of about 25 % in radial growth of subalpine *Pinus cembra* during the last century. Fertilization due to increased nitrogen deposition (Psenner and Nickus 1986; Smidt and Mutsch 1993) must also be considered as a possible growth stimulator. However, it should be noted that needle nitrogen contents are usually higher in trees within the timberline ecotone as compared to those of trees growing at lower elevation sites (Körner 1989). Furthermore, as there is evidenced that nitrogen limitation is not considered to be of particular importance in trees at timberline (Tranquillini 1979), Nicolussi et al. (1995) concluded that nitrogen deposition presently is insufficient to explain the observed trend in growth increment, which began long before nitrogen deposition at treeline tended to increase within the last 20 to 30 years (Psenner and Nickus 1986).

12.4 Climate warming

Greenhouse gas emissions can increase radiative forcing (Wuebbles et al. 1999) and there is extensive amount of evidence that the Earth's climate has warmed during the last century (Jones et al. 1998) and global change models predict a further increase in mean air temperature of 1.4 to 5.8 °C in the next century (IPCC 2001). These changes appear to be most pronounced in the European Alps (Diaz and Bradley 1997) where minimum temperatures tend to increase more than mean temperatures (Beniston et al. 1997). On a local scale this trend could also be documented for the Central Austrian Alps and changes appear to be greatest during spring and summer (Table 12.1, Fig. 12.4). Low temperatures during the dormant season *per se* have only little effects on carbon fluxes in conifers (Tranquillini 1959a, b; Havranek and Tranquillini 1995; Wieser 1997, 2000; Wieser and Bahn

2004; Wieser et al. 2005), soil CO_2 efflux (Wieser 2004), and the overall carbon balance of forest ecosystems within the timberline ecotone in the central European Alps (Wieser and Stöhr 2005). However, one has to take into account that one of the most noticeable effects of higher mean air temperatures on timberline associated forest ecosystems is a lengthening of the snow free period due to rising spring temperatures (Table 12.1, Fig 12.4; see also Groisman et al. 1994). At the timberline the central Austrian Alps the growing season extended from 168 ± 12 days during the period 1972 to 1985 (Havranek 1987) to 196 ± 23 days during the years 1994 to 2004 (Wieser 2004).

Table 12.1. Annual mean, winter (December-February), spring (March-May), summer (June-August), and autumn (September-November) temperature differences and standard deviation (°C) at timberline on Mt. Patscherkofel (Klimahaus Research Station), Austria 1950 m a.s.l. between 1963-1994 and 1995-2004. *difference statistically significant at $p < 0.05$ and at $**p < 0.01$; (two tailed unpaired Student *t*-test, n=32 against n=10 years.

	Mean temperature 1963-1994	Mean temperature 1995-2004	Difference
Annual mean	2.1±0.9	3.1±0.7	+1.0**
Winter	-4.0±1.5	-3.4±0.9	+0.6
Spring	0.3±1.4	1.7±0.9	+1.4**
Summer	8.9±1.2	10.5±1.6	+1.6*
Fall	3.5±1.3	3.5±1.2	0

To illustrate the impact of warming to our understanding of the future carbon sink strength of timberline associated forests in the central European Alps Wieser and Stöhr (2005) developed an empirical model which links climatic variables with gross primary production and ecosystem respiration, respectively. Calculations based on these two gas flux models clearly show that a 1.0 °C increase in mean annual temperature will increase total annual gross primary production and ecosystem respiration of a timberline associated *Pinus cembra* forest by about 15 and 10 %, respectively; and thus leading to an increase in net ecosystem production of 5 % as compared to the present situation (see Chap. 6.5). Measurements on carbon fluxes in a Scots pine forest ecosystem in eastern Finland also support these calculations (Zha et al. 2004) as there is evidence that under future warmer conditions the effects of an increasing rate of gross primary production are not masked by an increasing ecosystem respiration (Grace and Rayment 2000). Moreover, after six years of artificial soil warming stemwood production in a boreal Norway spruce stand has been shown to be up to 115 % higher than in untreated control plots (Strömgren and

Linder 2002). These observations strongly suggest that a future warmer climate and its impact on growing season length (cf. also Bergh and Linder 1999) may increase the carbon sequestration of high altitude and high latitude forest ecosystems.

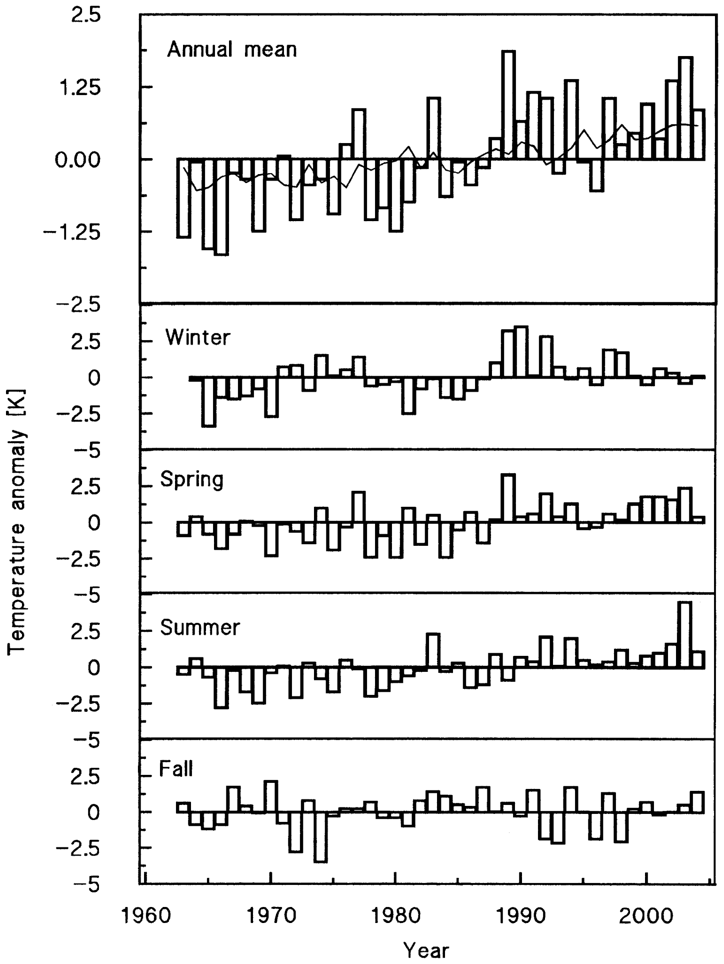

Fig. 12.4. Global warming on the northern hemisphere (thin line; source: Climate Research Unit, University of East Anglia, Aug. 2005. http//www.cru.uea.ac.uk) and variation in annual mean, winter (December-February), spring (March-May), summer (June-August), and autumn (September-November) air temperature changes.(open bars) from 1963 to 2004 at the Mt. Patscherkofel (Klimahaus Research Station), Austria 1950 m a.s.l.

An increase in air temperature, and hence probably also in needle temperature, may also increase evapotranspiration and hence may also lead to changes in the distribution of individual species (Mitchell et al. 1990; Zolbrod and Peretson 1999). However, although an upward advancement of low stature vegetation has recently been noted at alpine sites (Hofer 1992; Grabherr et al. 1994) the alpine treeline seems to behave in a "conservative" way (Grace et al. 2002). Hättenschwiler and Körner (1995) failed to find evidence for an upward migration of pine seedlings in the timberline ecotone of the Swiss Alps, which strongly suggests that the alpine treeline seems to be dependent on species interactions, which are fairly more linked to local site conditions, soil, and relief (see Chap. 2.3) than to moderate climate warming.

12.5 Ultraviolet-B radiation

In the context with other global environmental changes such as elevated atmospheric CO_2 concentration and increasing temperature solar ultraviolet-B (UV-B) radiation within the 280 - 320 nm waveband became a topic of increasing concern because of the stratospheric ozone depletion observed since the 1970s (Madronich et al. 1995). Independent from latitude the increase in surface level UV-B correlates with stratospheric ozone depletion (Kerr and McElroy 1993; WMO 1998; Fig. 12.5).

Although UV-B exposure decreases with increasing latitude, the relative increase in solar UV-B radiation shows an opposite trend, because stratospheric ozone depletion is higher in the arctic than at lower latitudes (Caldwell et al. 1999). This is probably more important for the timberline ecotone than absolute radiation levels (Björn et al. 1998; Turunen and Laltola 2005). Since 1981 in the European Alps the increase in the biologically active UV-B radiation has been approximated as 1 % per year in spring (Blumthaler and Ambach 1990). Elevation above sea level, solar angle, reflectance from snow and ice (albedo), differences in cloud cover, and aerosols are also important site factors influencing the UV-B level at a local scale (Blumthaler et al. 1994, 1997; De Lucia et al. 1991; Jokela et al. 1995; Gröbner et al. 2000).

Although UV-B radiation reaching the earth's surface comprises less than 0.5 % of the total solar energy reaching the earth's surface UV-B is of potential biological significance for plants because radiation in this waveband can damage nucleic acids and proteins (Caldwell et al. 1999). However, most plants growing in high radiation environments have developed several means of protection against high UV-B, which are in general characteristic for Alpine and also for Arctic plants (Caldwell et al. 1982). One adaptation mechanism is manifested in leaf optical properties. Reflectance of UV-B radiation on needle surfaces is generally less than 10 % (DeLucia et al. 1992), but tends to increase with increasing elevation (Richardson et al. 2001).

Due to a thick lignified epidermis and a thick cuticular layer transmittance of UV-B into the mesophyll is almost zero in conifer needles (Gilles and Vidaver 1990; DeLucia et al. 1991; Day et at. 1992; Day 1993; Schnitzler et al. 1996). Flavonoids and related phenolic compounds accumulate in epidermal cells of conifers (Starck et al. 1988; Schnitzler et al. 1996; Fischbach et al. 1999) where they protect inner cell layers from UV-B damage (Flint et al 1985; Fernbach and Mohr 1990; Jordan et al. 1992; Mackerness et al. 1996). The composition of flavonoids also changes with elevation. For instance, *Pinus sylvestris* populations growing at high altitudes are rich in prodelphinidin, while low altitude populations are rich in taxifolin (Laracine-Pittet and Lebreton 1988). The cuticular wax layer itself however, may not protect against UV-B radiation, because removal of the surface wax in fully developed conifer needles did not increase UV-B penetration into the mesophyll of various conifer species as shown by Day et al. (1992).

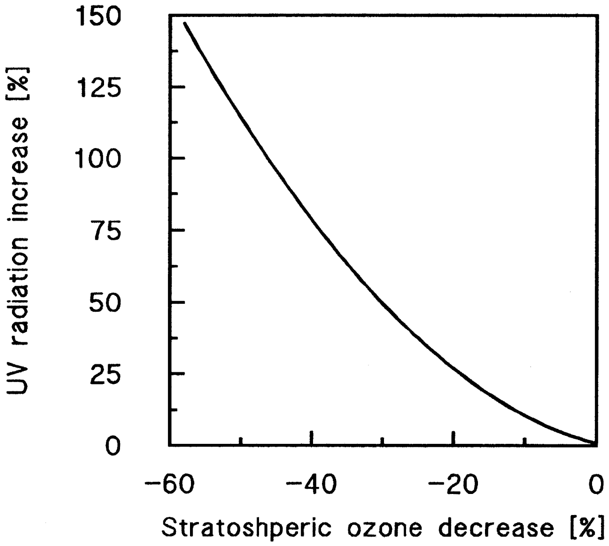

Fig. 12.5. Stratospheric ozone depletion in relation to the increase in surface-level biologically ultraviolet radiation. (Modified after WMO 1998.)

In addition, beside an increase in UV-B absorbing compounds, an increase in leaf thickness, which is a common feature along elevational gradients (Stover 1944; Fiella and Penuelas 1999; Körner 2003), may also be an important mode of protection against UV radiation (Fiella and Penuelas 1999). Furthermore, trees at the timberline have been shown to own thicker leaves as compared to trees in the closed forest below (Benecke et al. 1981; Hurtin and Marshall 2000). This suggests that conifers at high elevation sites may use increasing needle thickness as a strategy to stay away from UV-B damage.

Due to the open canopy of timberline associated forests the trees receive a relatively large amount of both high UV-B and photosynthetically active radiation which might increase the formation of reactive oxygen species in the cells. However, antioxidative defence systems counteracting adverse effects of reactive oxygen species enable plants to withstand oxidative stress and changes in the defence capacity of conifers is indicated by diurnal and seasonal cycles of antioxidants (Polle and Rennenberg 1994). A light and temperature dependent increase in apoplastic ascorbate (Wieser et al. 1996) and glutathione (Schupp and Rennenberg 1988) in needles of *Picea abies* causes diurnal cycles with high concentrations during the day and low concentrations during the night. Seasonal fluctuations are evident by high wintertime concentrations of ascorbate (Esterbauer et al. 1980) and glutathione (Esterbauer and Grill 1978; Schupp and Rennenberg 1988; Polle and Rennenberg 1992) due to their role in protecting evergreen foliage against winter injury. Thus, because antioxidant levels follow daily and seasonal cycles they may also provide protection against high UV-B radiation naturally occurring in the timberline ecotone during noon and in spring (Laakso and Huttunen 1998). The idea that a specific increase in antioxidants in conifer needles might provide a forward defence against oxidative stress is also supported by the observation that foliar ascorbate and glutathione contents are significantly higher in trees growing at high elevations (Polle and Rennenberg 1992, 1994; Polle et al. 1995; Tausz et al. 1997; Hecke et al. 2003) where plants are chronically exposed to higher oxidative stress including ambient UV-B radiation as compared with lower elevations.

When conifer needles were exposed to a shock treatment with high UV levels, the needles were remarkably UV resistant (Cline and Salisbury 1966). While most of the herbaceous plants died at UV levels between 4 and 42 J m^{-2} (1-5 cal cm^{-2}) the tolerance limits for conifers lay between 410 and 12300 J m^{-2} (100-3000 cal cm^{-2}). Under a xenon lamp with a total irradiance of 1400 W m^{-2} including a UV component within the 200 and 380 nm waveband of 26.5 W m^{-2} (≅ the radiation above the Mars atmosphere) *Pinus nigra* needles survived for 400 hours while *Zea mays* leaves were already damaged after only 15 hrs of exposure.

Experimental exposure of conifers to elevated UV-B radiation under controlled conditions in greenhouses and growth cabinets (Sullivan 2005) and in field grown trees in their natural habitat (Laakso and Huttunen 1998) did not significantly affect photosynthesis and biomass production. In addition, the response of high-altitude plants to elevated UV-B under controlled conditions is often less pronounced as compared to plants from low elevation sites, which clearly indicates that trees growing within the timberline ecotone are well adapted to UV-B (Tranquillini 1979; Turunen and Latola 2005). Because UV shielding and repair systems appear to be adequate to prevent damage, trees at the timberline will not suffer significantly in growth and reproduction when solar UV-B radiation will increases by up to 30 % in response to increasing stratospheric ozone depletion (Caldwell et al. 1999). In addition, trees at the timberline have developed also a co-tolerance to several other stress factors naturally occurring at high elevations and thus, acclimation and adaptation to the harsh environmental conditions can also increase the tolerance to UV-B radiation (Turunen and Latola 2005).

References

Ammer U, Breitsameter J, Kraus W, Zander J (1996) Der Beitrag des Bergwaldes zum Schutz gegen Oberflächenabfluss und Bodenabtrag. In: Scheiring H (ed) Das Bergwaldprotokoll: Forderungen an den Wald – Forderungen an die Gesellschaft. Blackwell Wissenschafts-Verlag Berlin, Wien, pp 9-31

Amt der Tiroler Landesregierung (2005) Zustand der Tiroler Wälder. Untersuchungen über den Waldzustand und die Immissionsbelastung. Berichte an den Tiroler Landtag 2005, Innsbruck

Aulitzky H (1994) Musterbeispiele vermeidbarer Hochwasser- und Lawinen. Veröffentlichungen der Kommission für Humanökologie der Österreichischen Akademie der Wissenschaften 4: 69-96

Aulitzky H (1996) Beispiele vermeidbarer Hochwasser- und Lawinenschäden. Tagungsband der Österreichischen Gesellschaft für Ökologie. Symposium Naturkatastrophen hausgemacht?, pp 25-57

Benecke U, Schulze E-D, Matyssek R, Havranek WM (1981) Environmental Control of CO_2-assimilation and leaf conductance in *Larix decidua* Mill. I. a comparison of contrasting natural environments. Oecologia 50: 54-61

Beniston M, Diaz HF, Bradley RS (1997) Climate change at high elevation sites: an overview. Climate Change 36: 233-251

Bergh J, Linder S (1999) Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands. Global Change Biology 5: 245-253

Bernoulli M, Körner Ch (1999) Dry matter allocation in treeline trees. Phyton 39: 7-12

Bianco J, Dalstein W (1999) Abscisic acid in needles of *Pinus cembra* in relation to ozone exposure. Tree Physiology 19: 787-791

Björn LO, Callaghan TV, Gehrke C, Johanson U, Sonensson M, Gwynn-Jones D (1998) The problem of ozone depletion in northern Europe. Ambio 27: 275-279

Blumthaler M, Ambach W (1990) Indication of increasing ultraviolet-B flux in alpine regions. Science 248: 206-208

Blumthaler W, Ambach W, Salzgeber M (1994) Effects of cloudiness on global and diffuse UV irradiance in a high-mountain area. Theoretical and Applied Climatology 50: 23-30

Blumthaler W, Ambach W, Ellinger R (1997) Increase in solar UV radiation with altitude. Journal of Photochemistry and Photobiology 39: 130-134

Bortenschlager S, Oeggl K (2000) The Iceman and his natural environment. The man in the ice, vol 4. Springer, Wien, New York

Caldwell MM, Robbrecht R, Novak RS, Billings WD (1982) Differential photosynthetic inhibition by ultraviolet radiation in species fro the Arctic-alpine life zone. Arctic and Alpine Research 14. 195-202

Caldwell MM, Searles PS, Flint SD, Barnes PW (1999) Terrestrial ecosystem responses to solar UV-B radiation mediated by vegetation, microbes and abiotic photochemistry. In: Press MC, Scholers JD, Barker MG (eds) Physiological plant ecology. British Ecological Society, Blackwell, pp 241-262

Cernusca A (1977) Schipisten gefährden die Umwelt. Umschau 77: 109-112

Cernusca A (1978) Ecological changes on abandoned alpine pastures. Results of an interdisciplinary ecosystem analysis in the Gastein valley, central Alps. In: Cernusca A (ed) Ökologische Analysen von Almflächen im Gasteiner Tal. Veröffentlichungen des österreichischen MaB-Hochgebirgsprogramms Hohe Tauern, Band 2. Universitätsverlag Wagner, Innsbruck, pp 17-27

Cernusca A, Angerer H, Newesely C, Tappeiner U (1990) Ökologische Auswirkungen von Kunstschnee. Eine Kausalanalyse der Belastungsfaktoren. Verhandlungen der Gesellschaft für Ökologie 19: 746-757

Cline MG, Salisbury FB (1966) Effects of ultraviolet radiation on the leaves of higher plants. Radiation Botany 6: 151-163

Conrad H (1940) Beitrag zur urgeschuchtlichen Besiedlung des Engadins. Jahresbericht der Historisch-Aquitanischen Gesellschaft Graubündens 70: 1-40

Cornelissen JHC, Carnelli AL, Callaghan TV (1999) Generalities in the growth, allocation and leaf quality responses to elevated CO_2 in eight woody species. New Phytologist 141: 401-409

Curtis PS (1996) A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. Plant, Cell and Environment 19: 127-137

Dalstein L, Torti X, LeThiec D, Dizengremel P (2002) Physiological study of declining *Pinus cembra* (L.) trees in southern France. Trees 16: 299-305

Damm B (1998) Waldgrenze, Baumgrenze, Waldentwicklung und Siedlungstätigkeit in den Tauferer Bergen (Südtirol) während des Postglazials. Geoökodynamik 19: 19-42

Day TA (1993) Relating UV-B radiation screening effectiveness of foliage to absorbing-compound concentrations and anatomical characteristics in a diverse group of plants. Oecologia 95: 542-550

Day TA, Vogelman TC, DeLucia EH (1992) Are some plant forms more effective than others in screening out ultraviolet-B radiation? Oecologia 92: 513-519

DeLucia EH, Day TA, Vogelmann TC (1991) Ultraviolet-B radiation and the Rocky Mountain environment: measurement of incident light and penetration into foliage. Current Topics in Plant Biochemistry and Physiology 10: 32-48

DeLucia EH, Day TA, Vogelman TC (1992) Ultraviolet-B and visible light penetration into needles of two species of subalpine conifers during foliar development. Plant, Cell and Environment 15: 921-929

Diaz HF, Bradley RS (1997) Temperature variations during the last century at high elevation sites. Climate Change 36: 253-279.

Donaubauer E (1980) Über Pilzkrankheiten in Hochlagenaufforstungen. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien 129: 51-62

Esterbauer H, Grill D (1978) Seasonal variation of glutathione and glutathione reductase in needles of *Picea abies*. Plant Physiology 61: 119-121

Esterbauer H, Grill D, Welt R (1980) Der jahreszeitliche Rhythmus des Ascorbinsäuresystems in Nadeln von *Picea abies*. Zeitschrift für Pflanzenphysiologie 98: 392-402

Fernbach E, Mohr H (1990) Coaction of blue/ultraviolet-A light and light absorbed by phytochrome in controlling growth of pine (*Pinus sylvestris* L.) seedlings. Planta 180: 212-216

Fiella IT, Penuelas J (1999) Altitudinal differences in UV absorbance, UV reflectance and related morphological traits of *Quercus ilex* and *Rhododendron ferrugineum* in the Mediterranean region. Plant Ecology 145: 157-165

Fischbach RJ, Kossmann B, Panten H, Steinbrecher R, Heller W, Seidlitz HK, Sandermann H, Hertkorn N, Schnitzler J-P (1999) Seasonal accumulation of ultraviolet-B screening pigments in needles of Norway spruce (*Picea abies* (L.) Karst.). Plant, Cell and Environment 22: 27-37

Flint SD, Jordan PW, Caldwell MM (1985) Plant protective response to enhanced UV-B radiation under field conditions: leaf optical properties and photosynthesis. Photochemistry and Photobiology 41: 95-99

Gilles SL, Vidaver W (1990) Resistance to photodamage in evergreen conifers. Physiologia Plantarum 92: 148-153

Göbl F (1965) Die Zibenmykorrhiza im subalpinen Aufforstungsgebiet. Centralblatt für das Gesamte Forstwesen 82. 89-100

Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. Nature 369: 448

Grace J, Rayment M (2000) Respiration in the balance. Nature 404: 819-820

Grace J, Berninger F, Nagy L (2002) Impact of climate change on the treeline. Annals of Botany 90: 537-544

Graumlich LJ (1991) Subalpine tree growth, climate, and increasing CO_2: an assessment of recent growth trends. Ecology 72: 1-11

Gröbner J, Albold A, Blumthaler M, Cabot T, De la Casiniere A, Lenoble J, Martin T, Masserot D, Muller M, Philipoena R, Pichler T, Pougatch E, Rengarajan

G, Schmucki D, Seckmeyer G, Sergent C, Toure ML, Weihs P (2000) Variability of spectral solar ultraviolet irradiance in an alpine environment. Journal of Geophysical Research 102: 26991-27003

Groisman PY, Karl TR, Knight RW (1994) Observed impact of snow cover on the heat balance and the rise of continental spring temperatures. Science 263: 198-200

Handa T, Körner Ch, Hättenschwiler S (2005) A test of the treeline carbon limitation hypothesis by in situ CO2 enrichment and defoliation. Ecology 86: 1288-1300

Hättenschwiler S, Körner Ch (1995) responses to recent climate warming of *Pinus sylvestris* and *Pinus cembra* within their montane transition zone in the Swiss Alps. Journal of Vegetation Science 6. 357-368

Hättenschwiler S, Miglietta F, Raschi A, Körner Ch (1997) Thirty years of in situ tree growth under elevated CO_2: a model for future forest responses? Global Change Biology 3: 463-471

Hättenschwiler S, Handa T, Egli L, Asshof R, Ammann W, Körner Ch (2002) Atmospheric CO_2 enrichment of alpine treeline conifers. New Phytologist 156: 363-37

Havranek WM (1987) Physiologische Reaktionen auf Klimastress bei Bäumen an der Waldgrenze. In: Klima und Witterung im Zusammenhang mit neuartigen Waldschäden. GSF Bericht 10/87: 115-130

Havranek WM, Tranquillini W (1995) Physiological processes during winter dormancy and their ecological significance. In: Smith WK, Hinckley TM (eds) Ecophysiology of coniferous forests. Academic Press, San Diego, pp 95-124

Havranek WM, Wieser G, Bodner M (1989) Ozone fumigation of Norway spruce at timberline. Annales Sciencies Forestrier 46 Suppl.: 581s-585s

Hecke K, Tausz M, Gigele T, Havranek WM, Anfodillo T, Grill D (2003) Foliar antioxidants and protective pigments in *Larix decidua* Mill. from contrasting elevations in the Northern and Southern Tyrolean Limestone Alps. Forstwissenschaftliches Centralblatt 122: 368-375

Hofer HP (1992) Veränderungen in der Vegetation von 14 Gipfeln des Berninagebietes zwischen 1905 und 1985. Berichte Geobotanisches Institut der Eidgenössisch Technischen Hochschule Stiftung Rüber (Zürich) 58: 39-54

Holtmeier F-K (1986) Die obere Waldgrenze unter dem Einfluß von Kilma und Mensch. Abhandlungen aus dem Landesmuseum für Naturkunde 48: 395-412

Holtmeier F-K (1973) Geoecological aspects of timberlines in Northern and Central Europe. Arctic and Alpine Research 5, 2: A45-A54

Holtmeier F-K (1994). Introduction to the upper Engadin and its forest. In: Schmidt WC, Holtmeier F-K. (eds) Proceedings – In: Schmidt WC, Holtmeier F-K (eds) Proceedings – International workshop on subalpine stone pines and their environment: the status of knowledge; Sept. 5-11; St. Moritz, Switzerland. Tech. Rep. INT-GTR-309. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT, pp 9-17

Holtmeier F-K (2003) Mountain timberlines. Ecology, patchiness, and dynamics. Advances in Global Change Research, vol 14. Kluwer Academic Publishers, Dordrecht, Boston, London

Hurtin KR, Marshall JD (2000) Altitude trends in conifer leaf morphology and stable carbon isotope composition. Oecologia 123: 32-40

Innes JL (1991) High-altitude and high-latitude treegrowth in relation to past, present and future global climate change. Holocene 2: 168-173

IPCC (2001) Climate change 2001: the scientific basis. Cambridge University Press, Cambridge

Jokela K, Lesczynzki K, Visuri R, Ylantilla L (1995) Increased UV exposure in Finland. Photochemistry and Photobiology 62: 101-107

Jones PD, Wigley TML, Folland CK, Parker DE, Angelli JK, Jebedeff S, Hansen JE (1988) Evidence of global warming in the last decade. Nature 332: 791

Jordan BR, He J, Chow WSM, Anderson JM (1992) Changes in mRNA levels and polypeptide subunits of rib lose 1,5-bisphosphate carboxyl's in response to supplementary ultraviolet-B radiation. Plant, Cell and Environment 15: 91-98

Keeling CD, Whorf TP, Whalen M, van der Plicht J (1995) Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. Nature 375: 666-670

Keller G (1997) Mykosoziologische Studie über die Mycorrhizapilze der Zirbe. Schriftenreihe der Forstlichen Bundesversuchsanstalt Wien, FBVA-Bericht 98

Kerr J, McElroy CT (1993) Evidence for large scale upward trend of ultraviolet-B radiation linked to ozone depletion. Science 262: 1032-1034

Kienast F, Luxmore RL (1988) Tree-ring analysis and conifer growth responses to increased atmospheric CO_2. Oecologia 76: 487-495

Körner Ch (1989) The nutritional status of plants from high altitudes. A worldwide comparison. Oecologia 81: 379-391

Körner Ch (2003) Alpine plant life: functional plant ecology of high mountain ecosystems, 2nd edn. Springer, Berlin

Kronfuss H, Havranek WM (1999) Effects of elevation and wind on the growth of *Pinus cembra* L. in a subalpine afforestation. Phyton 39: 99-106

Laakso K, Huttunen S (1998) Effects of the ultraviolet-B radiation (UV-B) on conifers : a review. Environmental Pollution 99: 319-328

Laracine-Pittet C, Lebreton P (1988) Flavonoid variability within *Pinus sylvestris*. Phytochemistry 27: 2663-2666

Leidlmair A (1983) Landeskunde Österreich. Paul List Verlag München

Mackerness SA-H, Butt PJ, Jordan BR, Thomas B (1996) Amelioration of ultraviolet-B-induced down regulation on mRNA levels for chloroplast proteins, by high irradiance, is mediated by photosynthesis. Journal of Plant Physiology 148: 100-106

Madronich S, McKenzie RL, Caldwell MM, Björn LO (1995) Changes in the ultraviolet radiation reaching the earth's surface. Ambio 24: 143-152

Marenco A, Gouiget H, Nenelec P, Pages J-P (1994) Evidence of a long term increase in tropospheric ozone from Pic du Midi data series: consequences, positive radioactive fording. Journal Geophysical Research 99: 16617-16632

Matyssek R, Havranek WM, Wieser G, Innes JL (1997) Ozone and the forests in Austria and Switzerland. In: Sandermann H, Wellburn AR, Heath RL (eds) Forest decline and ozone. A comparison of controlled changer and field experiments. Ecological Studies, vol 127. Springer, Berlin, Heidelberg, New York, pp 95-134

Mayer H (1970) Waldgrenzstuduien in den Berchtesgadener Alpen. Mitteilungen der Oatalpin-dinarischen Gesellschaft für Vegetationskunde 11: 109-120

Mitchell JFB, Manabe S, Meleshko V, Tokioka T (1990) Equilibrium climate change – and its implications for the future. In: Houghton JT, Jenkins GT (eds) Climate change: the IPCC scientific assessment. Cambridge University Press, Cambridge, pp 131-164

Nicolussi K, Bortenschlager S, Körner Ch (1995) Increase in tree-ring width in subalpine *Pinus cembra* from the central Alps that may be CO_2-related. Trees 9: 181-189

Norby RS, Wullschleger SD, Gunderson CA, Johnson DW, Ceulemans R (1999) Tree response to rising CO_2 in field experiments: implications for the forest future. Plant, Cell and Environment 22: 683-714

Patzelt G (1996) Modellstudie Ötztal – Landschaftsgeschichte in Hochgebirgsraum. Mitteilungen der Österreichischen Geographischen Gesellschaft 138: 53-70

Paulsen J, Weber UM, Körner Ch (2000) Tree growth near treeline: abrupt or gradual reduction with altitude? Arctic, Antarctic, and Alpine Research 32: 14-20

Polle A, Rennenberg H (1992) Field studies on Norway spruce trees at high altitudes: II. Defense systems against oxidative stress in needles. New Phytologist 121: 635-642

Polle A, Rennenberg H (1994) Photooxidative stress in trees. In: Foyer CH, Mullineaux PM (eds) Causes of photooxidative stress and amelioration of defense systems. CRC Press, Boca Raton, pp 199-218

Polle A, Wieser G, Havranek WM (1995) Quantification of ozone influx and apoplastic ascorbate content in needles of Norway spruce trees (*Picea abies* L., Karst) at high altitude. Plant, Cell and Environment 18: 681-688

Psenner R, Nickus U (1986) Snow chemistry of a glacier in the Central Eastern Alps (Hintereisferner, Tyrol, Austria). Zeitschrift für Gletscherkunde und Glaziologie 22: 1-18

Richardson AD, Berlyn GP, Gregorie TG (2001) Spectral reflectance of *Picea rubens* (Pinaceae) and *Abies balsamifera* (Pinaceae) needles along an elevational gradient, Mt. Moosilauke, New Hampshire, USA. American Journal of Botany: 667-676

Rolland C, Petitcolas V, Michalet P (1998) Changes in radial tree growth of *Picea abies*, *Larix decidua*, *Pinus cembra*, and *Pinus uncinata* near the alpine timberline since 1750. Trees 13: 40-53

Saxe H, Ellsworth DE, Heath J (1998) Tree and forest functioning in an enriched CO_2 atmosphere. New Phytologist 139: 396-436

Schiechtl H (1954) Die Folgen der Entwaldung am beispiel des Finsingtales in Nordtirol. Centralblatt für das Gesamte Forstwesen 73: 13-28

Schneider J, Loibl W, Spangl W (1996) Kumulative Ozonbelastung der Vegetation in Österreich. UBA Report 96-107, Bundesministerium für Umwelt, Wien.

Schnitzler J-P, Jungblut TP, Feicht C, Kofferlein M, Langebartels C, Heller W, Sandermann HJr (1996) UV-B induction of flavenoid biosynthesis in Scots pine (*Pinus sylvestris* L.) seedlings. Trees 11: 162-168

Schupp R, Rennenberg H (1988) Diurnal changes in the glutathione content of spruce needles (*Picea abies* L.). Plant Science 57: 113-117

Smidt S (1998) Risk assessment for air pollutants and forested areas in Austria, Bavaria, and Switzerland. Environmental Science and Pollution Research 1: 25-31

Smidt S, Gabler K (1994) Entwicklung von SO_2-, NO_2, und Ozonjahresmittelwerten in Österreich. Centralblatt für das Gesamte Forstwesen 111: 183-196

Smidt S, Mutsch F (1993) Messung der nassen Freilanddeposition an alpinen Höhenprofilen. Proceedings International Symposium „Schadstoffeinträge aus der Atmosphäre und Waldbodenbelastung in den Ländern der ARGE ALP und ALPEN ADRIA“. GSF Bericht 39/93: 21-29

Stark D, Heilemann J, Mömkern M, Wary V (1988) Cell wall-conjugated phenolics from coniferous leaves. Phytochemistry 27: 3517-3521

Stern R (1966) Der Waldrückgang im Wipptal. Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn 70

Stiny J (1910) Die Muren. Versuch einer Monographie mit besonderer Berücksichtigung der Verhältnisse in den Tiroler Alpen. Wagner´sche Universitäts-Buchdruckerei, Innsbruck,

Stover EL (1944) Varying structure of conifer leaves in different habitats. Botanical Gazette 47: 176-189

Strömgren M, Linder S (2002) Effects of nutrition and soil warming on stemwood production in a boreal Norway spruce stand. Global Change Biology 8: 1195-1204

Sullivan JH (2005) Possible impacts of changes in UV-B radiation on North American trees and forests. Environmental Pollution 137. 380-389

Tausz M, Grill D, Jimenez MS, Morales D (1997) A physiolpogical comparison between environmental effects on Canary pine in Tenerife and Norway spruce in Austria. In. Mohren GMJ, Kramer K, Sanbate S (eds) Impacts of global change on tree physiology and forest ecosystems. Kluwer Academic Publishers, Dortrecht, Boston, London, pp 103-110

Tausz M, Bytnerowicz A, Weidner W, Arbaugh MJ, Padgett P, Grill D (1999) Changes in free radical scavengers describe the susceptibility of *Pinus ponderosa* to ozone in southern Californian forests. Water, Air, and Soil Pollution 116: 249-254

Tausz M, Šircel JH, Grill D (2004) The glutathione system as stress marker in plant ecophysiology – is a stress-response concept valid? Journal of Experimental Botany 55: 1955-1962

Tranquillini W (1959a) Die Stoffproduktion der Zirbe (*Pinus cembra*) an der Waldgrenze während eines Jahres. I. Standortklima und CO_2-Asimilation. Planta 54: 107-129

Tranquillini W (1959b) Die Stoffproduktion der Zirbe (*Pinus cembra*) an der Waldgrenze während eines Jahres. II. Zuwachs und CO_2-Bilanz. Planta 54: 130-151

Tranquillini W (1979) Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. Ecological Studies, vol 31. Springer, Berlin, Heidelberg, New York

Turunen M, Latola K (2005) UV-B radiation and acclimation in timberline plants. Environmental Pollution 137: 390-403

Vecchi R, Valli G (1999) Ozone assessment in the southern part of the Alps. Atmospheric Environment 33: 97-109

Volgger E (1995) Zur Ozonempfindlichkeit der europäischen Lärche (*Larix decidua* Mill.) an der Waldgrenze. Diploma thesis, Innsbruck University

Vollenweider P, Ottiger M, Günthardt-Goerg MS (2003) Validation of leaf ozone symptoms in natural vegetation using microscopical methods. Environmental Pollution 124: 101-118

Volz A, Kley D (1988) Evaluation of the Montsouris series of ozone measurements made in the nineteenth century. Nature 332: 240-242

Walther G-R, Beißner S, Pott R (2005) Climate change and high mountain vegetation shifts. In Broll G, Keplin B (eds) Mountain ecosystems. Studies in treeline ecology. Springer, Berlin, Heidelberg, pp 77-95

Wieser G (1997) Carbon dioxide gas exchange of cembran pine (*Pinus cembra*) at the alpine timberline during winter. Tree Physiology 17: 473-477

Wieser G (2000) Seasonal variations of leaf conductance in a subalpine *Pinus cembra* during the winter months. Phyton 40: 185-190

Wieser G (2004) Seasonal variation of soil respiration in a *Pinus cembra* forest at the upper timberline in the Central Austrian Alps. Tree Physiology 24: 475-480

Wieser G, Bahn M (2004) Seasonal and spatial variation in woody-tissue respiration in a *Pinus cembra* tree at the alpine timberline in the Central Austrian Alps. Trees 18: 576-580

Wieser G, Havranek WM (1993) Ozone uptake in the sun and shade crown of spruce: quantifying the physiological effects of ozone exposure. Trees 7: 227-232

Wieser G, Havranek WM (2001) Effects of ozone on conifers in the timberline ecotone. In. Huttunen S, Heikkilä H, Bucher J, Sundberg B, Jarvis P, Matyssek R (eds) Trends in European forest tree physiology research. Tree Physiology, vol 2. Kluwer Academic Publishers, Dortrecht, Boston, London, pp 115-125

Wieser G, Stöhr D (2005) Net ecosystem carbon dioxide exchange dynamics in a *Pinus cembra* forest at the upper timberline in the central Austrian Alps. Phyton 45: 233-242.

Wieser G, Havranek WM, Polle A (1996) Effects of ambient and above ambient ozone concentrations on mature conifers in the field. In: Kärenlampi L, Skärby L (eds) Critical levels for ozone in Europe: testing and finalizing the concepts. UN-ECE Workshop Report. University of Kuopio, Department of Ecology and Environmental Science, pp 183-190

Wieser G, Tausz M, Wonisch A, Havranek WM (2001) Free radical scavengers and photosynthetic pigments in *Pinus cembra* L. needles as affected by ozone exposure. Biologia Plantarum 44: 225-232

Wieser G, Gigele T, Pausch H (2005) The carbon budget of an adult *Pinus cembra* tree at the alpine timberline in the Central Austrian Alps. European Journal of Forest Research 124: 1-8

Wieser G, Manning WJ, Tausz M, Bytnerowicz A (2006) Evidence for potential impacts of ozone on *Pinus cembra* L. at mountain sites in Europe: An overview. Environmental Pollution: 139: 53-58

WMO (1998) World meteorological organization scientific assessment of ozone depletion 1998

Wuebbles DJ, Jain A, Edmonds J, Harvey D, Hayhoe K (1999) Global change: state of their science. Environmental Pollution 100: 57-86

Zha T, Kellomaki S, Wang KY, Rouvinen I (2004) Carbon sequestration and ecosystem respiration for 4 years in a Scots pine forest. Global Change Biology 10: 1492-1503

Zolbrod N, Peretson DL (1999) Response of high-elevation forests in the Olympic Mountains to climate change. Canadian Journal of Forest Research 29: 1966-1978

13 Synopsis

Gerhard Wieser[1] and Michael Tausz[2]

[1]Institut für Naturgefahren und Waldgrenzregionen, BFW, Innsbruck
[2]School of Forest and Ecosystem Science, University of Melbourne

The timberline ecotone stretches from the *forest line* – the upper limit of a continuous forest canopy – to the *tree limit*. The latter represents the transition zone where the balance between abiotic and biotic environmental factors and the tolerance of trees becomes limiting for tree growth.

Temperature is suggested to be the key environmental factor in determining the transition from forests to alpine shrub and grassland and determining the upper limit of tree life. Many physiological aspects are influenced directly or indirectly by the temperature regime at the alpine timberline and, as shown in the previous chapters, several of these aspects may be directly limiting tree growth and survival. Therefore, tree life at the timberline obviously exists close to a number of physiological limits, which interact to determine the position of the alpine timberline and modulate the upper border of tree life at a fine scale.

In principle there are several, partly interrelated causes for the upper survival limit of trees in the Alps with seasonally fluctuating climate. Among them

- an insufficient carbon balance,
- a limitation to cell growth and tissue formation,
- and climatic stress

are probably the most important ones.

G. Wieser and M. Tausz (eds.), Trees at their Upper Limit, 219–223.

13.1 Carbon assimilation and allocation

As detailed in Chap. 6 the net photosynthetic capacity of trees in the timberline ecotone is similar to that of their relatives at lower elevation sites. However, due to evolutionary temperature adaptation the foliage of trees at the timberline displays a lower ecotype specific temperature optimum of net photosynthesis than leaves from trees at lower elevation sites. Similarly, when measured at the prevailing temperature trees experience in their local habitat, the night-time respiration rates from trees at the timberline match those from lower elevation sites. Thus, genetic and physiological adaptation to the climate at timberline plays a positive role. The annual carbon gain of leaves is mainly limited by the length of the growing season and the supply of irradiance and not by temperature during daylight hours.

The overall annual carbon budget of trees at timberline is also balanced fairly well and the carbon use efficiency (the ratio of net primary production to photosynthetic carbon gain) of trees at timberline is within the range reported for trees in forest ecosystems at lower elevation sites. In addition, carbon allocated into storage and reserves tends to increase with altitude showing a maximum at the tree limit.

On the other hand, factors tending to limit dry matter production predominate at timberline, as there is evidence that dry matter production declines with increasing altitude. However, there is no additional decline in dry matter production across the timberline ecotone above the forest limit although trees develop a more stunted morphology

Thus, taken together, currently available evidence on carbon accumulation and allocation does not support the hypothesis that the upper limit of tree growth in the European Alps is determined by an insufficient carbon assimilation and /or allocation.

13.2 Growth

At the timberline temperature has a direct effect on the formation of new tissues and tree growth (Chap. 7). Because of their life form, trees at timberline are well coupled to the atmosphere and thus experience lower tissue temperatures than adjacent low stature vegetation. As a consequence, their apical meristems do not profit from radiative warming. In addition, in adult trees below the *kampfzone* the tree’s canopy prevents heat flux to their rooting zone and hence soil temperatures are also lower as compared to krummholz-mats and other low stature vegetation.

Shoot and radial growth, as well as root growth is reduced substantially or even ceases when temperatures drop below 5–7 °C. Thus, limitation to new tissue growth by temperature is suggested to be the key factor in determining the transition from forests to alpine shrub and grassland and determining the upper limit of tree life.

Soil temperatures also influence above ground metabolism and growth, which emphasizes the relevance of root-zone temperature for physiological processes at the treeline. Higher proportional biomass partitioning to roots of high altitude ecotypes is considered to be an adaptation to unfavourable climatic conditions, where nutrient supplies are limited due to cold soils and the related low metabolic activity of micro organisms.

These findings therefore favour the view that the combination of apical meristems being coupled to atmospheric conditions and the development of cold soils under trees may limit the life-form tree, whenever temperatures during the growing season fall below a threshold necessary for growth and development.

13.3 Environmental factors (climatic stress)

Most of the environmental factors causing stress are of local origin and therefore, overall are of secondary importance for the occurrence of trees, although they will contribute to a finer-tuning of the treeline position in the Alps.

Winter causes extreme demands on water relations of trees protruding the winter snow cover (Chap. 8). Transpirational water loss combined with prevented water uptake by roots due to frozen stem bases and soil causes *winter desiccation* or *frost drought* which is a common phenomenon at the upper border of the timberline. Insufficient maturation of cuticles and buds during the preceding summer and needle damage and wax abrasion caused by winter wind may also contribute to excess water loss. Winter desiccation can finally lead to needle mortality and thus may reduce carbon assimilation and hence also growth of trees.

Late spring frosts are also a threat recurrently causing *frost damage* to new shoots of treeline trees (Chap. 10). However, frost damage *per se* does not appear to threaten the survival of trees at the alpine timberline. By partial injuries it rather contributes to the distorted growth of trees, especially in the krummholz belt.

Trees at the timberline are prone to *photo-oxidative stress*, caused by a number of environmental factors, such as the combination of high irradiance with low temperatures, elevated UV, elevated atmospheric ozone concentrations, and others (Chap. 11). Photo-oxidative stress can cause a sustained decrease in carbon fixation and hence potentially limit photosynthetic production. Defence systems against oxidative stress become relatively more important to trees at the timberline and will consume further resources. Although the overall importance of photo-oxidative stress in determining timberline positions is unclear, it certainly contributes to local fine-tuning by inhibiting tree establishment beyond existing canopies.

Anthropogenic changes to the lower atmosphere and related *global change* effects are likely to modify environmental stress factors at the timberline and add novel ones, such as increased ozone concentrations, increased UV-B, and elevated atmospheric CO_2 (Chap. 12). It is at present highly uncertain as to how such changes may affect trees at the timberline ecotone and the timberline position itself. While elevated ozone seems to be related with the decline of timberline trees at some field sites, experimental evidence corroborates clear ozone effects only at exposures to levels considerably higher than currently present. However, there is growing evidence that interactions of ozone with other environmental factors must be taken into account. Defence and shielding of Alpine timberline trees from UV-B seems adequate even to cope with increasing levels related to stratospheric ozone depletion (Chap. 12).

Although elevated CO_2 and related climate warming seems to increase photosynthetic production and carbon sequestration in timberline trees, it is at present unlikely that this will have a direct effect on the timberline position, which seems to be determined by local competition between species more than a moderate climate warming (Chap. 12).

13.4 What determines the timberline?

Thus it seems to be clear that the timberline position at a given site will depend on a multitude of factors: Temperature caused limitations in (above and below ground tissue) growth, combined with incomplete tissue maturation, and finally - even if occurring only locally – also an inadequate resistance to climatic stress factors are interconnected and determine the timberline on top of historic and edaphic conditions. Acting in interrelation they dictate the climate driven transition from the life form tree to low stature vegetation such as dwarf-shrubs, alpine grassland, and meadows in the European Alps.

However, future climate change might be of paramount importance for tree and low stature vegetation distribution within the timberline ecotone in the European Alps, where low temperatures generally limit carbon metabolism, growth, soil microbial activity and even ecosystem fluxes. Thus, natural thermal gradients within a common given environment provide excellent opportunities for ecophysiological field research with respect to the adaptation of various plant life forms to predicted future global warming. Natural thermal gradients due to effects of altitude (macro-scale) and effects of relief (micro-scale) are powerful tools for global change research. In addition, when compared to artificial manipulative warming experiments vegetation within the timberline ecotone is well adjusted to the natural soils and the rhizosphere with respect to long term trends (decades, centuries) at the whole ecosystem level.

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