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Gerhard Wieser, Rainer Matyssek, Roland Luzian, Peter Zwerger, Peter Pindur, et al.. Effects of atmospheric and climate change at the timberline of the Central European Alps. *Annals of Forest Science*, 2009, 66 (4), <10.1051/forest/2009023>. <hal-00883473>

HAL Id: hal-00883473

<https://hal.science/hal-00883473v1>

Submitted on 11 May 2020

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Effects of atmospheric and climate change at the timberline of the Central European Alps

Gerhard WIESER^{1*}, Rainer MATYSSEK², Roland LUZIAN¹, Peter ZWERGER¹, Peter PINDUR³,
Walter OBERHUBER⁴, Andreas GRUBER⁴

¹ Dept. Alpine Timberline Ecophysiology, Federal Research and Training Centre for Forests, Natural Hazards and Landscape, Rennweg 1, 6020 Innsbruck, Austria

² Dept. of Ecology/Ecophysiology of Plants, Technische Universität München/Weihenstephan, Am Hochanger 13, 85354 Freising, Germany

³ Institut für Stadt- und Regionalforschung, Österreichische Akademie der Wissenschaften, Postgasse 7, 1010 Wien, Austria

⁴ Institute of Botany, University of Innsbruck, Sternwartestraße 15, 6020 Innsbruck, Austria

(Received 21 July 2008; accepted 19 December 2008)

Keywords:

Alpine timberline /
treeline /
global warming /
CO₂ /
ozone /
water balance /
carbon gain

Mots-clés :

limite supérieure alpine de la forêt /
limite de croissance des arbres /
réchauffement global /
CO₂ /
ozone /
bilan hydrique /
gain de carbone

Abstract

• This review considers potential effects of atmospheric change and climate warming within the timberline ecotone of the Central European Alps. After focusing on the impacts of ozone (O₃) and rising atmospheric CO₂ concentration, effects of climate warming on the carbon and water balance of timberline trees and forests will be outlined towards conclusions about changes in tree growth and treeline dynamics.

• Presently, ambient ground-level O₃ concentrations do not exert crucial stress on adult conifers at the timberline of the Central European Alps. In response to elevated atmospheric CO₂ *Larix decidua* showed growth increase, whereas no such response was found in *Pinus uncinata*. Overall climate warming appears as the factor responsible for the observed growth stimulation of timberline trees.

• Increased seedling re-establishment in the Central European Alps however, resulted from invasion into potential habitats rather than upward migration due to climate change, although seedlings will only reach tree size upon successful coupling with the atmosphere and thus losing the beneficial microclimate of low stature vegetation.

• In conclusion, future climate extremes are more likely than the gradual temperature increase to control treeline dynamics in the Central European Alps.

Résumé – Effets des changements atmosphériques et des changements climatiques à la limite supérieure de la forêt en Europe dans les Alpes centrales.

• Cette étude examine les effets potentiels des changements atmosphériques et du réchauffement climatique au sein de l'écotone qui constitue la limite supérieure de la forêt dans les Alpes centrales en Europe. Après avoir mis l'accent sur les effets de l'ozone (O₃) et de l'augmentation des concentrations atmosphériques du CO₂, les effets du réchauffement climatique sur le bilan de carbone et le bilan hydrique des arbres et des forêts à la limite supérieure de la forêt seront présentés en vue de tirer des conclusions sur l'évolution de la croissance des arbres et sur les dynamiques de la limite supérieure de la forêt.

• Actuellement, les concentrations en O₃ de l'air ambiant au niveau du sol n'exercent pas un stress critique sur les arbres adultes à la limite supérieure de la forêt dans les Alpes centrales en Europe. En réponse à des concentrations élevées en CO₂ *Larix decidua* a montré une augmentation de la croissance, alors qu'une telle réponse n'a pas été trouvée chez *Pinus uncinata*. Globalement, le réchauffement climatique apparaît être le facteur responsable de la stimulation de la croissance observée chez les arbres à la limite supérieure de la forêt.

• Toutefois, l'augmentation de la réinstallation des semis dans les Alpes centrales en Europe est le résultat de l'invasion d'habitats potentiels plutôt qu'une migration en altitude due aux changements climatiques, bien que les semis atteindront seulement la taille des arbres après un couplage réussi avec l'atmosphère et donc perdant le microclimat favorable d'une végétation basse.

• En conclusion, les phénomènes climatiques extrêmes futurs sont plus susceptibles de contrôler les dynamiques de limite supérieure de la forêt, que l'augmentation progressive de la température dans les Alpes centrales en Europe.

* Corresponding author: Gerhard.Wieser@uibk.ac.at

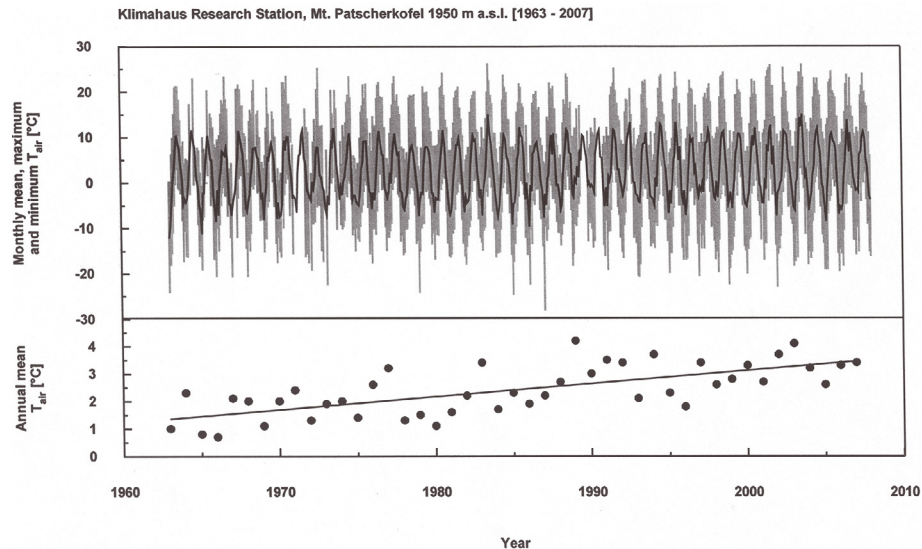


Figure 1. Top: Monthly average (solid line), maximum and minimum (grey bars) air temperature from January 1963 throughout December 2007 and (bottom) mean annual air temperature at the Mt. Patscherkofel Klimahaus Research Station, Austria, 1950 m a.s.l.

1. INTRODUCTION

The alpine timberline designates the limit of forest growth as imposed by the environmental specificities of this ecotone. Rather than being an abrupt boundary, this timberline typically forms a transition zone between the *forest line* (i.e. the upper limit of closed-canopy conditions) and the *tree line* (disappearance of life form tree) mediating to the *krummholz* zone above (Däniker, 1923; Holtmeier, 2003; Slatyer and Noble, 1992; Tranquillini, 1979; Wardle, 1974; Wieser and Tausz, 2007). The *tree limit* is defined by tree heights of 2 to 3 m (Körner, 2007; Wieser and Tausz, 2007), which ensure tree crowns to be well coupled with the atmosphere (also in winter, as protruding above the snow cover). Above the tree line, tree and shrub species are deformed to *krummholz*, characterized by stunted habit, either hugging the ground or attaining, at most, the height of the snow cover (Tranquillini, 1976). Hence, such plants experience microclimates similar to dwarf plants which dominate the *alpine zone* at the next higher vegetation belt (Grace et al., 2002).

Although at a given site the position of the timberline depends on a multitude of factors, in particular, temperature-caused limitations in growth (Körner, 1998), such restrictions are interrelated with incomplete tissue maturation, sometimes inadequate resistance to climatic stress, which altogether determines the altitudinal distribution limit of trees (Wieser and Tausz, 2007). A number of hypotheses have been posed to functionally explain the occurrence of timberlines (Körner, 2003). The multi-factorial interactions govern the transition from the life form tree to low-stature vegetation such as dwarf-shrubs and alpine grasslands.

Awareness currently increases about timberline-associated forest ecosystems because these are expected to undergo significant alterations due to climate warming and changes in the chemical composition of the lower atmosphere (Grace et al.,

2002; Holtmeier and Broll, 2007; Walther et al., 2005, Wieser and Tausz, 2007). Taking into account that growth and regeneration of trees within the timberline ecotone is mainly controlled by temperature (Körner, 2003), global warming is supposed to cause both an upward advancement of trees beyond the present tree limit (Walther, 2003) and denser forests below the forest limit (Grace et al., 2002). Such changes may have important implications on biogeochemical cycles and probably also on biodiversity within the timberline ecotone as ample evidence exists about climate warming by about 0.6 °C during the last century (Jones et al., 1998). Global change models predict even further temperature increase by 1.4 to 5.8 °C during the upcoming decades (IPCC, 2007). Such changes may be most pronounced in the European Alps (Beniston et al., 1997; Diaz and Bradley, 1997). Data from the timberline ecotone in the Central Austrian Alps show that during the last decade mean annual air temperature was higher, on average, by 1 °C as compared to the period before (Fig. 1) and changes appear to be greatest during spring (+1.4 °C) and summer (+1.6 °C) as compared to fall (0 °C) and winter (+0.6 °C). The overall warming is associated with changes in snow cover volume and duration (Hantel et al., 2000; Beniston et al., 2003). Due to increasing surface and air temperatures especially in spring (Groisman et al., 1994), the length of the growing season has markedly increased during recent years (Beniston et al., 2003; Hantel et al., 2000; Menzel and Fabian, 1999). In addition, winter rains will probably increase, whereas precipitation deficits may occur during the later part of the growing season (Breda et al., 2006; Brunetti et al., 2006). Moreover, other factors of climate change such as enhancements in atmospheric CO₂ concentration as well as tropospheric ozone may interact in concert with climate warming.

In addition, for millennia humans have influenced the timberline ecotone (Patzelt, 1995) as accessible slopes of moderate inclination were often deforested to gain seasonally used

pasture land (Holtmeier, 1973; Leidlmair, 1983). As a consequence, this impact has significantly lowered the natural tree-line by 150 to 300 m to below the postglacial *potential* climatic *treeline* (Holtmeier 1986, 1994). For that reason, it is uncertain whether the present *actual* timberline in the European Alps reflects equilibrium between climate and tree internal eco-physiological factors.

This paper summarizes the present knowledge about climate change at the timberline ecotone. Focus will be on the Central European Alps, as geographical variation in meso-climate and interference by Mediterranean, oceanic and continental influences (Beniston et al., 1977) hinder to draw a unique scenario for the whole European Alps (cf. also Theurillat and Guisan, 2001). After examining the impact of an altered atmospheric chemistry on the physiological behaviour of timberline trees, we will address possible effects of climate warming on tree carbon gain with respect to foliage type (deciduous vs. evergreen). Consequences for net primary production, growth, and water balance will be discussed, emphasizing potential effects of climate warming and land use change on the upward migration of trees and forest expansion.

2. ALTERED ATMOSPHERIC CHEMISTRY

2.1. Effects of ozone

During the last century the chemical composition of the lower troposphere has drastically changed over Europe. Ground-level ozone (O_3) concentrations have at least doubled and annual means nowadays range between 40 and 50 $nL L^{-1}$ (Stockwell et al., 1997). High-altitude forests generally experience higher O_3 levels (less O_3 destruction through NO_x , stratospheric O_3 intrusions, less re-circulation of polluted air masses) than forests at low elevation (Smidt, 1993; Herman et al., 2001) so that also O_3 uptake rates of trees are higher (Wieser et al., 2000). Nevertheless, there is no indication at present that ground level O_3 affects the net carbon gain of timberline trees (Häsler et al., 1991; Matyssek et al., 1997). O_3 fumigation experiments conducted at the forest limit in the central Austrian Alps showed that long lasting mean O_3 concentrations lower than 100 $nL L^{-1}$ did not significantly affect the carbon gain adult *Picea abies*, *Pinus cembra*, and *Larix decidua* trees after exposure throughout one growing season (Havranek et al., 1989; Wieser and Havranek, 2001; Volgger, 1995; Wieser et al., 2006). This is attributable to the detoxification capacity of oxygen radicals which is greater in timberline than lowland trees (Hecke et al., 2003; Polle and Rennenberg, 1992; Polle et al., 1992; Tausz et al., 1998) because high altitude plants are generally exposed to higher oxidative stress due to lower temperature, higher irradiance and higher O_3 concentration. Apoplastic ascorbate concentration in spruce needles was shown to be 25 to 75% higher at timberline than at elevations below 1000 m a.s.l. (Polle et al., 1995). Moreover, conifers at the timberline possess lower specific leaf area (SLA, leaf area per unit dry mass; Benecke et al., 1981; Hurtin and Marshall, 2000; Richardson et al., 2001; Wieser

and Tausz, 2007). High antioxidant levels at low SLA are apparently conducive to low O_3 sensitivity as observed in timberline provenances of *Picea abies* (Havranek et al., 1990) and *Larix decidua* (Volgger, 1995), as O_3 susceptibility positively correlates with SLA in parallel with decreasing antioxidant levels (cf. Matyssek et al., 2008a). Such findings indicate the ambient ground-level O_3 concentration per se to not exert crucial stress on timberline trees of the Central European Alps (Matyssek et al., 1997). In the absence of evident O_3 injury on timberline trees in the Central Austrian Alps (Matyssek et al., 1997), one-year-old needles of *Pinus cembra* trees in declining stands in the southern (more maritime) French Alps showed symptoms of yellowing and defoliation (Bianco and Dalstein, 1999; Dalstein et al., 2002) which were attributable to O_3 impact (Vollenweider et al., 2003). Thus, the action of O_3 must be evaluated in concert with other environmental factors which altogether determine the tree's sensitivity to O_3 .

2.2. Effects of elevated CO_2

The rise in atmospheric CO_2 concentration, having reached approximately 380 $\mu L L^{-1}$ at present, at a current rate of 1–2 $\mu L L^{-1} year^{-1}$, is another global phenomenon (Keeling et al., 1995; Keeling and Whorf, 2005). Three years of free-air CO_2 enrichment at the timberline in Switzerland proved light-saturated net photosynthesis of 30-year-old *Larix decidua* and *Pinus uncinata* trees to be significantly higher under elevated CO_2 than of control trees under ambient CO_2 concentration (Handa et al., 2005; Hättenschwiler et al., 2002). Non-structural carbohydrates were also increased under elevated CO_2 , suggesting that it is not carbon gain that presently limits tree growth at the timberline but the rate at which glucose can be utilized (Grace et al., 2002). As this latter rate is temperature-driven, low temperature rather than CO_2 supply was acknowledged to limit tree growth at high altitude (Körner, 2003). Hence, warming rather than elevated CO_2 is likely to shift the timberline towards higher elevation as compared with the current situation (see below).

Nevertheless, CO_2 enhancement caused a significant stimulation in lateral shoot growth and a cumulative four-year response of 41% in radial stem increment of deciduous *Larix decidua* whereas no such response was observed in evergreen *Pinus uncinata* (Handa et al., 2005, 2006). The difference in branch growth perhaps relates to the contrasting leaf habits of these two tree species (Cornelissen et al., 1999). Furthermore, if the observed growth response to elevated CO_2 depends on foliage type it is likely that other factors such as temperature and hence the length of the growing season might also be involved in the observed growth stimulation of deciduous larch as compared to evergreen pine (cf. also Crawford, 2008). One needs to caution, however, that even three years of experimental CO_2 enhancement (Handa et al., 2005; Hättenschwiler et al., 2002) might be too limited at the timberline, characterised by short growing seasons that alternate with prolonged winter dormancy, to conclude about long-term responses (cf. Norby et al., 1999; Saxe et al., 1998). Evidence exist that CO_2 effects will decline over time due to metabolic acclimation

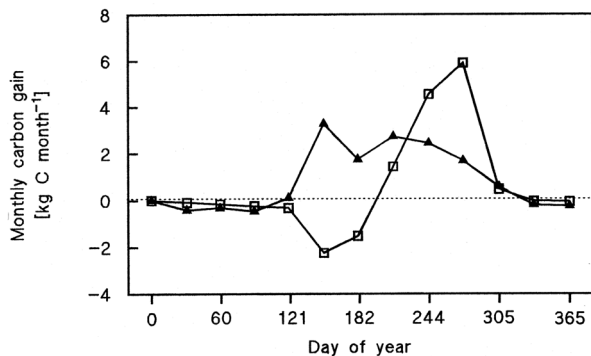


Figure 2. The seasonal course of the monthly carbon balance of a 95-year-old *Pinus cembra* (\blacktriangle) and a 65-year-old *Larix decidua* (\square) tree. Measurements were made at Mt. Patscherkofel (Klimahaus) Austria 1950 m a.s.l. (Modified after data from Wieser et al., 2005 and Havranek and Matyssek, 2005).

and age-related stand dynamics in competition for above and belowground resources (Hättenschwiler et al., 1997). Körner et al. (2005) also failed to find stimulation in growth and litter production after four years of CO₂ enrichment in mature temperate forest trees. In general, tree growth tends to acclimate to enhanced CO₂ supply upon long-term exposure, sustaining growth rates similar to those under the current, ambient CO₂ levels (Körner, 2006). This latter phenomenon supports the conclusion that tree growth is carbon-saturated already under the present environmental conditions (Körner, 2003). Timberline trees do not appear to be an exception, as their tissues are highly charged with photosynthates (Hoch and Körner, 2003; Hoch et al., 2002; 2003).

3. POTENTIAL IMPACTS OF CLIMATE WARMING

3.1. Effects on the carbon balance

The carbon balance is determined by the carbon uptake of the foliage and the carbon released via respiratory processes. The crucial factor for carbon fixation is the time span which enables a positive daily carbon balance. This time span is defined by the phenological dependence of ecophysiological processes. For example, *Larix decidua* does not unfold new needles before mid-June, whereas *P. cembra* achieves its maximum monthly carbon gain during the early growing season (Fig. 2). In addition, larch needles turn yellow in early October, whereas net photosynthesis in *P. cembra* ceases approximately one month later. Hence, the seasonal photosynthetic period of larch is 130 days on average as compared to approximately 180 days in *P. cembra* (Friedel, 1967; Havranek and Tranquillini, 1995). The shorter photosynthetic period in the deciduous *L. decidua* as compared to the evergreen *P. cembra* (Fig. 2) is however, compensated by a higher photosynthetic capacity and a higher daily and seasonal carbon gain (Tranquillini, 1962). Nevertheless, the carbon-use efficiency (i.e. ratio of gross photosynthesis vs. respiration; sensu Larcher, 2001) did not differ significantly and approached 7.0

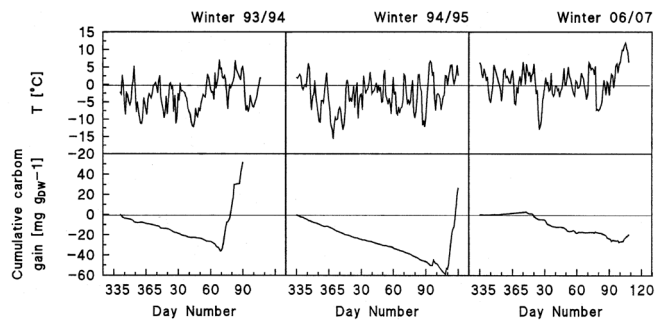


Figure 3. Seasonal patterns of daily mean air temperature (top) and cumulative carbon gain (bottom) of current to two-year-old needles of *Pinus cembra* at the timberline during winter (December, January, February) and early spring (March, April) of three years contrasting with respect to temperature. (Combined after data from Wieser, 1997 and Gruber et al., unpublished).

and 7.6 in *L. decidua* and *P. cembra*, respectively (Wieser and Tausz, 2007).

Since the growing season at the timberline is very short, small temperature differences at the beginning and the end of the snow-free period can have large effects on the annual carbon gain of evergreen conifers (Fig. 3). In general, the daily carbon balance of *Pinus cembra* needles is negative from December throughout March (Fig. 3; winter 1994–1995). During long-lasting warm periods in late winter, however, metabolic activity may increase (Fig. 3; winter 1993–1994) and daily carbon gain can reach up to 30% of summer levels. The winter of 2006–2007 was extraordinarily warm (average winter temperature Dec.–Feb. -1.1 °C) as compared to the 40-year average of -4.0 °C, and hence, significantly raised the carbon balance during the cold season (Fig. 3; winter 2006–2007). Moreover, Kronfuss and Havranek (1999) showed growth of *Pinus cembra* in a subalpine afforestation to be positively related to the length of the growing season.

Low temperature during winter dormancy by contrast hardly affects the annual carbon gain of conifers (Havranek and Tranquillini, 1995; Tranquillini, 1959a; 1959b; Wieser, 1997; Wieser and Bahn, 2004) and the overall carbon balance of timberline forests (Wieser and Stöhr, 2005). Relationships between gross primary production (GPP) and ecosystem respiration (ER) show under current climatic conditions in a *Pinus cembra* timberline forest of the Austrian Alps warm temperature during the growing season and their effects on ER to be key factors that limit net ecosystem production (Fig. 4; Wieser and Stöhr, 2005). Modelling suggests increase in mean annual temperature by 1.0 °C and its effect on growing season length to raise GPP and ER of this forest by about 15 and 10%, respectively, causing net ecosystem production to be enhanced by 5% relative to the present situation. Measurements in a boreal Scots pine forest in eastern Finland support this calculation (Zha et al., 2004), and warmer climatic conditions in future are expected to favour GPP more than ER (Grace and Rayment, 2000). Such a scenario may increase the carbon sequestration of timberline forest ecosystems (Bergh and Linder, 1999).

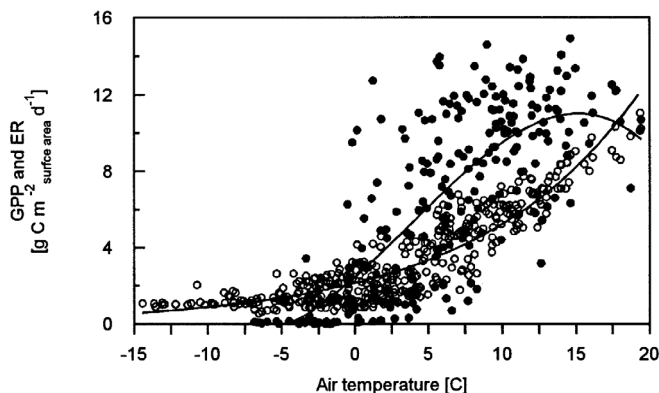


Figure 4. Temperature dependence of gross primary production (GPP; closed symbols) during the growing season and of ecosystem respiration (ER; open symbols) during an entire annual course in a 95-year-old *Pinus cembra* forest at Mt. Patscherkofel (Klimahaus), Austria, 1950m a.s.l. (Modified after data from Wieser and Stöhr, 2005).

Climate warming is also associated with changes in snow cover volume and duration (Beniston et al., 2003; Hantel et al., 2000) and precipitation patterns (Brunetti et al., 2006). Due to increasing surface and air temperatures, especially in spring (Groisman et al., 1994) the length of the growing season has markedly increased during recent years (Beniston et al. 2003; Hantel et al., 2000; Menzel and Fabian, 1999). For example, although not statistically significant, the growing season at the timberline of the central Austrian Alps amounted to 168 ± 12 days during the period of 1972 through 1985, and to 196 ± 23 days during 1994 through 2004 (Wieser and Tausz, 2007). Thus, with respect to carbon gain evergreen conifers at the timberline may benefit from future climate warming as compared to deciduous trees, when retaining their photoperiod (Larcher, 1994). Nevertheless, timing of budburst is a significant phenological event often involving high temperature for breaking winter dormancy in spring. Conversely, warm winters will increase the frequency of wet snow events, winter thaw and even snow-free periods, which will probably increase the number of freeze-thaw-cycles (Mayr et al., 2003) and, hence, the risk of embolisms in the xylem water (Mayr et al., 2007). Further risks for tree survival within the timberline ecotone may arise from early frost dehardening in spring upon warmer winter temperatures (Neuner, 2007) as well as frost drought (Oberhuber, 2004; Tranquillini, 1976). The latter is assumed to be one of the main causes for the upper limit of tree growth in high mountains outside the tropics (Baig and Tranquillini, 1980; Christersson et al., 1988; Schwarz, 1983; Sowell et al., 1982; Tranquillini, 1976; 1979; Turner, 1968) because of insufficient maturation of cuticles and buds during the preceding summer (Hadley and Smith, 1989; Holtmeier, 1974). Winter desiccation can occur throughout late winter and early spring when water losses by cuticular transpiration cannot be compensated due to frozen soil and limited water reserves in the above ground tissues (Hadley and Smith, 1990; Havranek and Tranquillini, 1995; Larcher, 1957; 1963;

1985; Michaelis, 1934a; 1934b; Sakai and Larcher, 1987; Tranquillini, 1976; 1979; 1982).

3.2. Effects on the water relations

Ample precipitation and moderate evaporative demand in general cause soil water content to be sufficiently high to meet the trees' water demand in high-elevation forests of the European Alps. As a consequence, timberline trees are rarely forced to restrict transpiration (Matyssek et al., 2008b; Tranquillini, 1979). In general, soil moisture at the timberline of the Central European Alps seldom drops below 20% vol. (Guggenberger, 1980; Gunsch, 1972; Neuwinger, 1970, 1980; Neuwinger-Raschendorfer, 1961; Wieser, 2004). Nevertheless, soil water availability can differ by micro-scale variation in soil depth and soil type so that soil water potential may locally be as low as -1 MPa (Anfodillo et al., 1998). Such low levels, however, are not critical for trees as they stay significantly above the vulnerability threshold of cavitation (Breda et al., 2006) through stomatal closure (Havranek and Benecke, 1978). Under ample soil water availability of a future warmer climate the water uptake capacity will possibly be improved through growth stimulation of the mycorrhizal root system and enlargement of its absorbing surface. In addition, water uptake may also be enhanced by rising soil temperature through lowered water viscosity (Kaufmann, 1975) and increased permeability of root membranes (Goldstein et al., 1985; Wan et al., 1999).

Conversely, limited soil water availability at sites with a shallow soil layer and increased evaporative demand upon climate warming may endanger trees through water imbalances, in particular, at their upper distribution limit where growth habit becomes stunted and deformed towards the *krummholz* zone (Holtmeier, 2003; Tranquillini, 1979; Wieser and Tausz, 2007). This latter zone already today is affected by temporary soil drought especially at wind exposed ridges and leeward sun-exposed slopes with thin soil layer (Aulitzky, 1963; 1984).

3.3. Effects on tree growth

Studies in the timberline ecotone of Central European Alps show increase in tree-ring widths after the so-called "little ice age" (1560 through 1870; Carrer and Urbinati, 2006; Paulsen et al., 2002; Rolland et al., 1998). Carrer and Urbinati (2006) proposed June temperature and precipitation to drive radial growth of *Larix decidua* in the Eastern Italian Alps during the last 200 y. Nicolussi et al. (1995) assumed atmospheric CO₂ enrichment to have stimulated tree-ring width of *Pinus cembra* in the central Austrian Alps during the second half of the 19th century. However, CO₂ enhancement was minor at that time. Furthermore, timberline trees are unlikely to be limited in their carbon balance, but they are by low temperature (see above; Körner, 1998, 2003). In addition to temperature, nitrogen deposition may be considered as a growth stimulator. However, time series analysis does not unveil positive correlation between annual ring width in the timberline ecotone of the

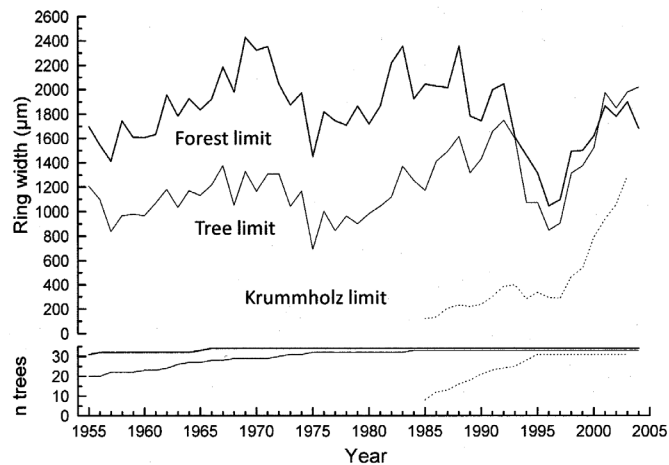


Figure 5. Radial stem growth of *Pinus cembra* from the forest limit (1950 m a.s.l.), the tree limit (2110 m a.s.l.) and the krummholz-limit (2180 m a.s.l.) on Mt. Patscherkofel during the period 1955–2004. Annual increments were measured on increment cores (2 radii per tree) taken at 1.3 and 1 m stem height (forest and tree limit, respectively) and on stem discs cut directly above soil surface at the krummholz-limit (stem height < 50 cm) (Selva and Oberhuber, unpublished).

Austrian and Swiss Alps (Nicolussi et al., 1995; Paulsen et al., 2000) and nitrogen deposition (Psenner and Nickus, 1986).

Most recently, dendroclimatological studies conducted within the timberline ecotone of the Central European Alps have shown, however, that radial stem growth is limited by low summer temperature (Büntgen, 2005; Carrer and Urbinati, 2004; Frank and Esper, 2005; Oberhuber, 2004). Still, variation between summer temperature and annual ring increment of *Picea abies* and *Larix decidua* was reported by Carrer and Urbinati (2006) and Büntgen et al. (2006). The latter authors related this variation in *Picea abies* to temperature-induced increase in late-summer drought that coincided with the recent trend of warming. Spatial variability in radial growth reductions of *Pinus cembra* at the timberline was also related in the 1990s to the occurrence of temporary, temperature-induced drought during the growing season (Oberhuber, 2004). Moderate increases in annual increments of *Pinus cembra* within the timberline ecotone of Mt. Patscherkofel (Tyrol, Austria) under the heat-wave of 2003 (Beniston, 2004; Schär et al., 2004), when mean summer temperatures exceeded the long-term mean of 1967–2002 by *c.* 4.1 °C and precipitation was reduced by 24%, might be explained accordingly (Fig. 5; cf. also Oberhuber et al., 2008). These interpretations are consistent with results of Anfodillo et al. (1998), who found that soils at the timberline became physiologically dry during the growing season, and high evaporative demand negatively affected the radial stem growth of *Pinus cembra*. Conversely, missing adequate growth response to recent climate warming may suggest the presence of temperature thresholds (Wilmking et al., 2004) and/or compensatory effects of climatic factors (Oberhuber et al., 2008; Pfeifer et al., 2005).

Besides air temperatures, soil temperature and associated root metabolism determine tree growth (Körner and Hoch, 2006). Low soil temperature as nowadays prevailing at the timberline are known to limit root growth (Häsler et al., 1999; Oberhuber, 2007; Tranquillini, 1973; Turner and Streule, 1983) and soil temperatures below 6 °C cause critical inhibition (Alvarez-Uria and Körner, 2007). This is meaningful to timberline trees with extensively mycorrhizal fine roots, as mycorrhization appears to be a pre-requisite of tree growth and survival at high altitude (Haselwandter, 2007; Moser, 1967).

Soil temperature influences above-ground metabolism and growth. In the timberline ecotone near Obergurgl, Austria (2070 m a.s.l.), Havranek (1972) found a linear correlation in situ between daily carbon gains of *Pinus cembra* seedlings and daily mean soil temperature at 10 cm depth of 0 to 7 °C ($C_{\text{day}} = 7.12 \times T_{\text{soil}} + 12.92$, $r^2 = 0.90$), while higher root zone temperatures do not limit photosynthesis. Moreover, artificial soil cooling reduced the diameter increment of stunted *Pinus cembra* trees near the *krummholz* limit at Mt. Patscherkofel, Innsbruck; (Oberhuber et al., unpublished observations). This finding is consistent with those of a soil warming experiment in a boreal spruce stand where stemwood production was significantly increased at elevated soil temperature (Strömngren and Linder, 2002).

4. TREELINE SHIFTS

As both growth and reproduction (Smith et al., 2003) of trees are controlled in the timberline ecotone by temperature, an upslope migration of tree species has been predicted under climate change (Grace et al., 2002; Holtmeier and Broll, 2007; Walther, 2003; and further reference therein). In fact, increased seedling establishment beyond the forest limit has been detected in the Swiss (Gehring-Fasel et al., 2007) and the Austrian Alps (Fig. 6; Luzian and Pindur, 2007). Nevertheless, the *treeline* assumed after the postglacial optimum was considerably lowered by human impacts (pasturing, mining; Holtmeier, 1973; Holtmeier and Broll, 2007; Leidlmair, 1983). Furthermore, recent changes in land-use management are considered to be a driving force for changes in ecosystem functioning and dynamics (Cernusca, 1999). Gellrich et al. (2007) observed a close relationship between land abandonment and forest re-growth in mountainous regions of Switzerland. At the Swiss timberline ecotone Gehring-Fasel et al. (2007) found that a large portion of seedling re-establishment resulted from invasion into potential habitats rather than an upward migration. Hättenschwiler and Körner (1995) and Paulsen et al. (2000) also failed to find evidence for upward migration of pine seedlings in the timberline ecotone of the Swiss Alps. Similar results are also reported from North America (Szeicz and MacDonald, 1995), Canada (Klasner, 2002) and the Ural Mountains in Russia (Shiyatov et al., 2005). Conversely, a recent advancement of the tree limit has been reported from the Swedish Scandes (Kullman, 2002). As such trends are lacking in the Alps (Gehring-Fasel et al., 2007) the treeline in the Central European Alps is said to behave in a “conservative” way (Grace et al., 2002). Tree advancement to higher elevations

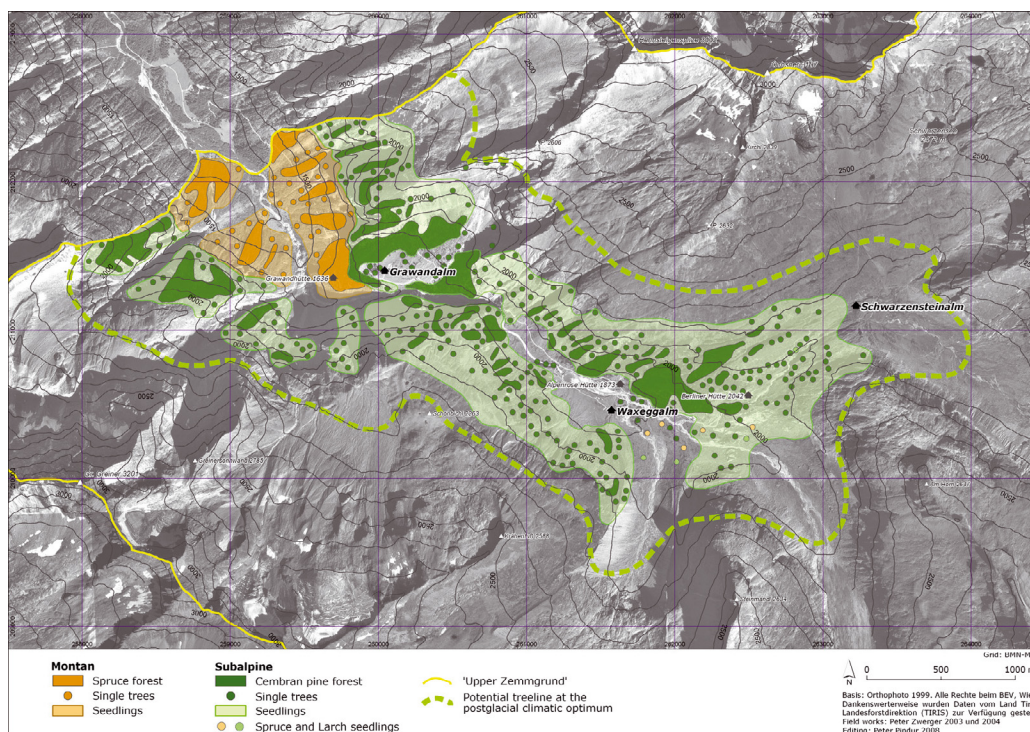


Figure 6. Actual distribution of montane Norway spruce (*Picea abies*) and subalpine cembra pine (*Pinus cembra*) forests, single trees, seedling re-establishment in an abandoned alpine pasture, and the reconstructed potential treeline during the postglacial optimum in the Oberer Zemmgrund, Zillertaler Alpen, Austria (modified after Zwinger and Pindur, 2007).

however, also depends on reproduction and survival of the recruitment (Smith et al., 2003). Although the reproduction has been less studied than growth in the given context, it has already been observed by Tranquillini (1979) that production of viable seeds above the forest limit often fails in years with a cool growing season. Warmth is likely to support viable seed production and seedling establishment. Tree advancement to higher elevations is coupled, in addition, with enhanced wind exposure. Hence, frost drought as well as needle abrasions by snow and ice (Holtmeier, 2003) are likely to increase as long as a tree population is too small to enhance snow accumulation (Kronfuss and Havranek, 1999). Thus, seedling establishment and survival will profit from sheltered micro-sites with respect to slope inclination and exposure (Smith et al., 2003). Differences in radiation dose resulting from topographic exposure are reflected in variations of soil and air temperature, snow cover duration, soil moisture, and consequently in the distribution of the vegetation (Aulitzky, 1963, 1984; Kronfuss, 1970; Larcher, 1985; Turner, 1993; Turner et al., 1975). Ingrown or advanced seedlings will only reach tree size when they can survive after being decoupled from the beneficial microclimate of low stature vegetation. Finally, tree development also depends on extreme events such as drought, severe frost during the growing season, frost drought, and even biotic stress by pathogens and herbivores. Thus severe climatic episodes are more likely than mean temperature to control tree population dynamics in timberline ecotone of the Central European Alps in future.

5. CONCLUSIONS

Increases in O_3 and CO_2 levels along with altered temperature and moisture regimes interact in their impact on timberline trees and forests in complex ways. There is no indication at present however, that ground level O_3 affects the net carbon gain of timberline trees. This kind of tolerance appears to be based on intrinsic adaptation to oxidative stress which increases with altitude (Wieser et al., 2001) not only because of higher ambient O_3 levels than at low elevation, but also due to lower temperature and higher irradiance. Hence, the capacity of detoxifying oxygen radicals is higher in trees at their upper distribution limit as compared to trees at low elevation (Polle et al., 1992; Hecke et al., 2003).

Elevated CO_2 hardly affects tree growth (Körner, 2003) as responsiveness depends on foliage type (Handa et al., 2005; 2006) so that low air temperature rather than carbon is the limiting factor of growth in trees at their upper distribution limit (Wieser and Tausz, 2007). With respect to carbon gain, trees and stands of the timberline ecotone will benefit from future climate warming as temperature-driven carbon loss by respiration is likely to be over-compensated by the concurrently increasing gross primary production (GPP; Wieser and Stöhr, 2005). Thus, the additional carbon acquired by timberline trees upon warming, including prolonged growing seasons, is available to various metabolic demands, especially, to match the subtle balance between above (light) and belowground resource sequestration (water, nutrients; Mooney

and Winner, 1991). In particular, competitiveness for below-ground resources is crucial for tree survival at the timberline (Calaway, 1998). Although future warming will improve the water uptake from soils, increasing evaporative demand may perturb the water balance at wind and sun-exposed sites with shallow soils. Such risk is indicated already today at the boundary between tree line and krummholz zone (Aulitzky, 1984).

The ample re-establishment of seedlings currently observable at the timberline of the Central European Alps occurs to a major extent in potential habitats of the respective tree species rather than upon upward-migration (Gehring-Fasel et al., 2007; Zwerger and Pindur, 2007). Invasion into such habitats is a consequence of the currently decreasing grazing pressure on pastures, which has suppressed forest up-growth throughout centuries at high altitude. This kind of habitat re-occupation suggests the tree line in the Central European Alps to behave in a conservative way (Grace et al., 2002). Nevertheless, prognoses of the impact of climate change on the productivity and sustainability of high altitude forest ecosystems will remain uncertain until experimental evidence from long-term field studies on the water and carbon balance in the timberline ecotone will become available.

Finally, one has to be aware that the alpine timberline in the Central European Alps is more susceptible to human impact such as land use changes and management practices than will likely be the case under expected climate change (Wieser and Tausz, 2007). In addition episodic extreme events by e.g. summer drought, severe frost during the growing season or biotic stress (by pathogens/herbivores) rather than the gradual temperature increase will control tree population dynamics within the timberline ecotone of the Central European Alps in the future environment.

Acknowledgements: Part of this research was supported by the Austrian (Federal) grants “Fonds für wissenschaftliche Forschung”, Project Nos. P18819-B03 and P19563-B16, “Stem growth and respiration of *Pinus cembra* at the timberline” and “Cambial activity and wood formation of Scots pine”, respectively.

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