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Review

Effects of Climate Change at Treeline: Lessons from Space-for-Time Studies, Manipulative Experiments, and Long-Term Observational Records in the Central Austrian Alps

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Abstract: This review summarizes the present knowledge about effects of climate change on conifers within the treeline ecotone of the Central Austrian Alps. After examining the treeline environment and the tree growth with respect to elevation, possible effects of climate change on carbon gain and water relations derived from space-for-time studies and manipulative experiments are outlined. Finally, long-term observational records are discussed, working towards conclusions on tree growth in a future, warmer environment. Increases in CO_2 levels along with climate warming interact in complex ways on trees at the treeline. Because treeline trees are not carbon limited, climate warming (rather than the rising atmospheric CO_2 level) causes alterations in the ecological functioning of the treeline ecotone in the Central Austrian Alps. Although the water uptake from soils is improved by further climate warming due to an increased permeability of root membranes and aquaporin-mediated changes in root conductivity, tree survival at the treeline also depends on competitiveness for belowground resources. The currently observed seedling re-establishment at the treeline in the Central European Alps is an invasion into potential habitats due to decreasing grazing pressure rather than an upward-migration due to climate warming, suggesting that the treeline in the Central Austrian Alps behaves in a conservative way. Nevertheless, to understand the altitude of the treeline, one must also consider seedling establishment. As there is a lack of knowledge on this particular topic within the treeline ecotone in the Central Austrian Alps, we conclude further research has to focus on the importance of this life stage for evaluating treeline shifts and limits in a changing environment.

Keywords: treeline; climate change; ecosystem manipulation; space-for-time substitution; long-term trends; Central Austrian Alps

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1. Introduction

Alpine treelines are obvious vegetation boundaries. In the Central Austrian Alps, treelines generally form an ecotone between the closed forest below and the treeless alpine zone above [1–8]. Due to abiotic climatic severity within this transition zone, trees become flagged and stunted, which leads to scrub-like trees higher up at the krummholz limit. Therefore, researchers commonly define treelines as the upper elevational limit of trees greater than 2 m in height [9,10]. Such a height ensures that tree crowns are well coupled to atmospheric conditions measured at a standard height (2 m) in weather stations. Further up to the krummholz limit, stunted bush-like trees experience microclimatic conditions that dominate the next higher altitudinal vegetation belt [11] and are characterized by low-growing vegetation (e.g., dwarf-shrubs, grassland, and meadows).

Generally, on a global and on a continental scale, the formation and the maintenance of treelines seem to be correlated with air or soil temperatures, although the altitudinal position of a treeline may vary with respect to site conditions. A world-wide survey indicates that in temperature limited ecosystems, a growing mean season air temperature of 5.5 to 7.0 °C constrains tree growth [12,13]. Moreover, in a global survey, a growing season mean soil temperature of 6.7 ± 0.8 °C in 10 cm soil depth matches the upper elevational limit of tree growth [14,15]. As in nature, such mean temperatures generally do not exist, and they should be considered as an indicator of heat deficiency rather than an underlying factor [2,3,16–18].

Presently, people have raised concern about treelines, because they are anticipated to experience considerable modifications due to global change, especially climate warming [11,19–24]. Global mean surface temperature has increased by about 0.6 ± 0.2 °C during the last century, and global change models predict a further increase by 1.4–5.8 °C for upcoming decades [25]. As observed changes appear to be most pronounced at high altitudes [26,27], and considering that alpine (high elevation) treelines are undoubtedly associated with heat deficiency, treeline ecotones are ideally suited for climate change monitoring [28].

Yet, knowledge of tree response to warming in treeline environments is critical for understanding potential alterations that will likely occur in a changing environment. Inference about future climate change typically relies on one of three approaches: space-for-time substitution, manipulative experiments, and long-term observational records.

- The space-for-time approach [15,29,30] uses variations of environmental conditions along altitudinal gradients, where warmer temperatures at lower elevations represent a likely future climate, while lower temperatures at higher elevations represent the present. Such variations in environmental conditions offer a great possibility for comparative research on ecophysiological adaptations to environmental alterations [24,29,31] with minimal confounding biogeographic influence and maximal interpretability [32]. Elevational transects are also considered as powerful tools to investigate climate-driven changes in tree growth [33,34].
- In-situ manipulative warming and rain shelter experiments are common methodologies for assessing the effects of rapid climate change [35]. They can be quite effective in simulating climate warming [36–39] and top soil drought [40,41] in high elevation forests. Compared to the space-for-time approach, such techniques provide an explicit control in simulating climate warming or artificial soil drought.
- Time series data [35] of tree growth and stable isotopes coupled with time series data of climate may facilitate a mechanistic understanding of climate-related influences on physiological processes, such as leaf gas exchange and stem wood formation, in response to recent climate warming and increasing CO_2 concentration [42].

This review summarizes the current knowledge about potential climate change effects on treeline-associated conifers. The focus is on the Central Austrian Alps, as geographical variations in mesoclimates and interferences by continental, oceanic, and Mediterranean influences hamper drawing a single scenario for the entire European Alps [24,43]. After examining the treeline environment and tree growth with respect to elevation, potential effects of climate change on carbon gain and water relations derived from space-for-time studies and manipulative experiments are examined. Finally, long-term observational records are discussed to evaluate effects of climate change on tree growth at their upper limit.

2. The Treeline Environment

The treeline environment in the Central Tyrolean Alps is characterized by harsh climatic conditions where short growing seasons alternate with periods of dormancy during the winter [44]. Figure 1 provides an example for seasonal changes in thermal conditions and precipitation within the treeline ecotone on Mount Patscherkofel in the Central Tyrolean Alps for the period 1961–1990. Due to recent climate warming, the mean annual air temperature during the last 28 years

(1991–2018) increased on average by 1.1 °C (i.e., to 3.1 °C) as compared to the previous 30 years (2.0 °C), while a considerable trend in air temperature was absent from 1925 to 1981 (Figure 1).

The temperature increase since 1982 apparently was most pronounced during spring (by 1.5 °C) and summer (by 1.5 °C) compared with autumn (by 0.3 °C) and winter (by 0.8 °C), implying early snowmelt in spring. Thus, the growing season increased by 4 ± 1 weeks during the last three decades [44]. Higher temperatures also intensified evaporative demand [45]. In contrast to temperature, total annual precipitation did not change significantly during the last 94 years (45).

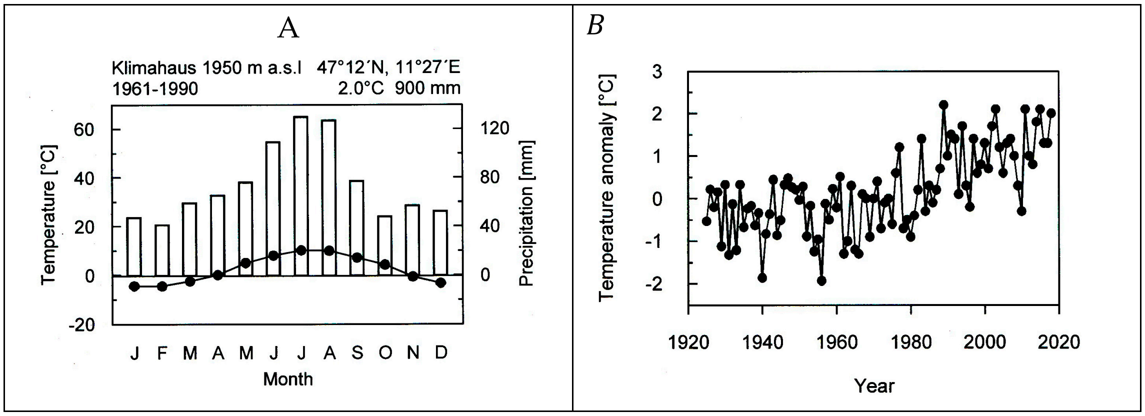

Figure 1. (**A**) Climate diagram (mean monthly temperature in lines and mean monthly precipitation in bars) and (**B**) temporal variation in mean annual air temperature during the period 1925–2018 relative to the 1961–1990 average at the treeline on Mount Patscherkofel. Compiled after [45] and [46].

Within the treeline ecotone soil depth, length of the growing season and the air temperature declined with increasing altitude, while soil temperature increased along the same elevational gradient [47,48]. The observed lower soil temperature at the forest limit can primarily be attributed to a closed canopy. The latter prevents radiative warming and soil heat flux of the rooting zone [8,15,47,49,50]. However, this is not the case in open stands at the tree and the krummholz limit. Moreover, in addition to altitude, slope angle and relief strongly determine the microclimate at any site within the treeline ecotone. Differences in radiation and wind velocity due to topographical features strongly influence soil development, soil temperature, snow cover duration, soil water availability, and, consequently, seedling establishment [49,51–56].

3. Tree Growth at Treeline

There is correlative and extensive evidence that temperature strongly affects tree growth and tissue formation at the treeline [29,36,50,57,58]. Height growth of *Pinus cembra* trees in the Tyrolean Alps has been shown to be highly correlated with growing season mean air temperature [58]. Moreover, radial stem and shoot increment of *P. cembra*, *Picea Abies,* and *Larix decidua* cease at temperatures lower than 5–7.5 °C [57,59,60]. Soil temperature also has been considered as a substantial factor restricting root growth [61] and influencing above ground metabolism [62]. Low soil nutrient availability (particularly nitrogen [63,64]) has also been attributed to terminating tree growth at the treeline [5,63], where decomposition and mineralization are limited by low soil temperatures [65–67]. Additionally, competition for below ground resources also may noticeably influence tree growth [68,69].

3.1. Height Growth

At the treeline in the Central Tyrolean Alps, researchers in [70] and [71] observed that cumulative height growth of naturally growing *P. cembra* trees was considerably lower in the kampfzone (i.e., the upper treeline belt) at 2194 m above sea level (a.s.l.) as compared to the upper end of the closed forest in 1995 m a.s.l (Figure 2). In subalpine (1730–2080 m a.s.l.) afforestations in the Sellrain and in the Schmirn Valley, Tyrol, Austria, height growth of young *P. cembra* [72,73], *P. abies,* and *L. decidua* [74] trees exceeding a height > 0.5 m also declined with elevation.

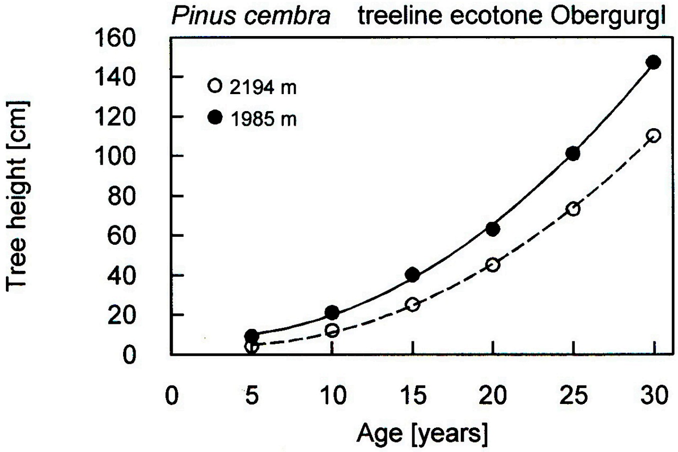

Figure 2. Cumulative height increment *of Pinus cembra* trees in relation to tree age at the forest limit [1985 m above sea level (a.s.l.); solid circles, solid line] and the krummholz limit (2194 m a.s.l.; open circles, dashed line) in Obergurgl, Ötztal, Tyrol, Austria. After [71].

Data in Table 1 show that the observed reduction in cumulative height growth with increasing elevation corresponds to a decline in the length of the growing season and an increase in wind velocity [72]. The effect of wind on height growth is more marked with increasing elevation because stands open up and trees are isolated from each other [5,18,74] and probably also because of a corresponding increase in wind damage with increasing elevation [3,18,72,75].

Table 1. Mean annual height increment of young *Pinus cembra* trees, mean growing season length, and mean wind velocity during the growing season at various altitudes in a subalpine afforestation in the Sellrain valley, Tyrol, Austria. Relative values are given as percentage of data from 1730 m a.s.l. After [72].

	Absolute values			**Relative values (%)**		
	1730 m	**1800 m**	**1900 m**	**1730 m**	**1800 m**	**1900 m**
Annual height increment (cm)	24.1	21.8	11.8	100	90	49
Growing season (days)	112	107	99	100	96	88
Wind velocity (m s^{-1})	1.2	1.3	3.1	100	108	258

In addition to elevation, exposure and microtopography strongly determine the microclimate at any site within the treeline ecotone and hence also influence height growth. For example, in the Sellrain valley, the cumulative height growth of 25-year-old *P. cembra* trees growing on a north-exposed slope 2000 m a.s.l was only 1.5 m as compared to 5.1 m in even aged *P. cembra* trees growing at 1900 m a.s.l on a south facing slope [72]. Similar differences in height growth with respect to microtopography have also been reported for *P. cembra* and *P. abies* trees in the Ötztal valley [71] and in the Schmirn valley [74], respectively. Height growth of seedlings, by contrast, is barely affected by topography and/or elevation [73,74]. This is because seedlings experience a microclimate comparable to that of short-stature plants that profit from life form-driven passive solar energy use, which facilitates canopy and soil heating [11].

3.2. Diameter Growth

Stem diameter growth also declines with increasing elevation, as shown for young *P. cembra* [73], *P. abies,* and *L. decidua* [74] trees in the Schmirn Valley, Tyrol, Austria. In general, the onset of cambial activity depends on the timing of snowmelt and the rise in air and soil temperature [47,76–78]. Reference [79] noted that cambial activity of *P. cembr*a at the treeline on Mount Patscherkofel began one week later at the krummholz limit at 2180 m a.s.l. than at the forest limit and at the treeline at 1950 and 2110 m a.s.l., respectively. Maximum radial increment as well as the termination of annual ring formation were independent of altitude and occurred at the same time throughout the treeline ecotone [47,79]. At the beginning of the growing season, higher numbers of cambial cells were found at sites with an open canopy (i.e., the treeline and the krummholz limit) as compared to the closed forest limit. Yet, root zone temperatures were also significantly higher in open stands as compared to the forest limit, indicating that soil temperature may influence tree growth at the treeline.

However, studies on the effect of artificial soil warming on tree growth in boreal forests [80,81] and in the Swiss [82] and the Austrian Alps [83] yielded ambiguous results, indicating species-specific responses with results ranging from no stimulation in growth to a strong growth stimulation. Three years of soil warming did not cause any response in stem diameter increment of 25-year-old *P. cembra* trees in an afforestation at 2150 m a.s.l. treeline in the Sellrain valley [38,84]. In the kampfzone on Mount Patscherkofel south of Innsbruck (2.180 m a.s.l.), root zone cooling and root zone warming hardly affected diameter growth of *P. cembra* [36]. The results of this study indicated that *P. cembra* reacted to soil cooling with a decline and to soil warming with an increase in radial stem increment when compared to control trees with soil temperature left un-manipulated. Observed differences in diameter growth, however, were not statistically significant [36], probably because—in addition to soil temperature—varying soil nutrient contents with respect to microtopography are also known to influence radial growth at the treeline [85].

In contrast to root-zone temperature manipulation, nitrogen fertilization and understory removal significantly increased radial growth of 25-year-old *P. cembra* trees in a subalpine afforestation at 2150 m a.s.l. [84]. Removal of belowground competition also improved seedling growth within the treeline ecotone [71] and tree growth in subalpine forests [68,69]. Moreover, restricted seedling and tree establishment above the current treeline has also been attributed to competition with neighboring low stature understory vegetation. [23,86–89]. However, evaluating long-term modifications in species interactions is still under debate [90,91] and awaits clarification for the Central European Alps. Neither understory removal nor nitrogen addition nor soil temperature manipulation considerably influenced seasonal dynamics in radial growth of *P. cembra* at the treeline [36,84].

Table 2. Growing season mean whole tree non-structural carbohydrate (NSC) pools (% dry matter) and the contribution of needle, branch, stem, and root NSC accumulation patterns (%) to whole tree NSC pools of *Pinus cembra* trees along an altitudinal transect between 1750 and 2175 m a.s.l. on Mount Patscherkofel. After [92].

Elevation (m)	Whole tree NSC pool (% dry weight)	Needle (%)	Branch (%)	Stem (%)	Root (%)
2175	4.7 ± 1.2	61	16	11	12
2100	4.0 ± 0.8	51	12	21	16
1950	3.9	49	7	26	18
1750	3.8 ± 1.1	47	7	25	21

Nevertheless, a decline in radial growth with increasing elevation was dominantly caused by a corresponding decline in temperature [93]. As already pointed out by [5], at cooler temperatures, there is a tendency for photosynthates to be transformed into non-structural carbohydrates (NSC) and their components (soluble sugars and starch rather than cellulose), which in turn may limit diameter growth. Studies on mobile carbohydrates in *P. cembra* trees along a south facing 425 m elevation transect from the closed forest at 1750 m a.s.l. up to the krummholz limit at 2175 m a.s.l. [92] indicated that growing season mean whole tree NSC pools increased with elevation (Table 2).

The observed increase in growing season mean whole tree NSC may be attributed to an increase in leaf mass with elevation [71,94], as needles contained the largest NSC fraction of the whole tree (Table 2).

4. Water and Carbon Relations within the Treeline Ecotone

4.1. Water Relations

Ample precipitation (Figure 1) and moderate evaporative demand usually cause soil water availability to be sufficient to meet the tree water demand within the treeline ecotone. Furthermore, minimum tree water potentials during the growing season have been found to stay considerably above a critical value, causing xylem cavitation risks [95,96]. In general, transpiration of conifers at the treeline shows a very pronounced response to increasing evaporative demand in terms of solar radiation and vapor pressure deficit under appropriate water supply [97,98]. Multiple regression analyses showed that, at the forest limit and at the treeline, solar radiation had a similar effect on tree water loss as vapor pressure deficit [97]. At the krummholz limit, by contrast, vapor pressure deficit had a bigger effect on tree water loss than irradiance. In addition, the absence of a closed canopy at the krummholz limit triggered an intensification in fundamental atmospheric processes [7,98].

Slope angle is a determinant of topo- and microclimatic related differences in solar radiation [98] and wind velocity [7,98]. At the krummholz limit, higher wind velocities than those at the forest limit and at the treeline (Table 1) cause a wind-induced clustering of the needles [99,100]. Consequently, the response of the stomata is impaired due to partial stomatal narrowing [99,100] (Figure 3).

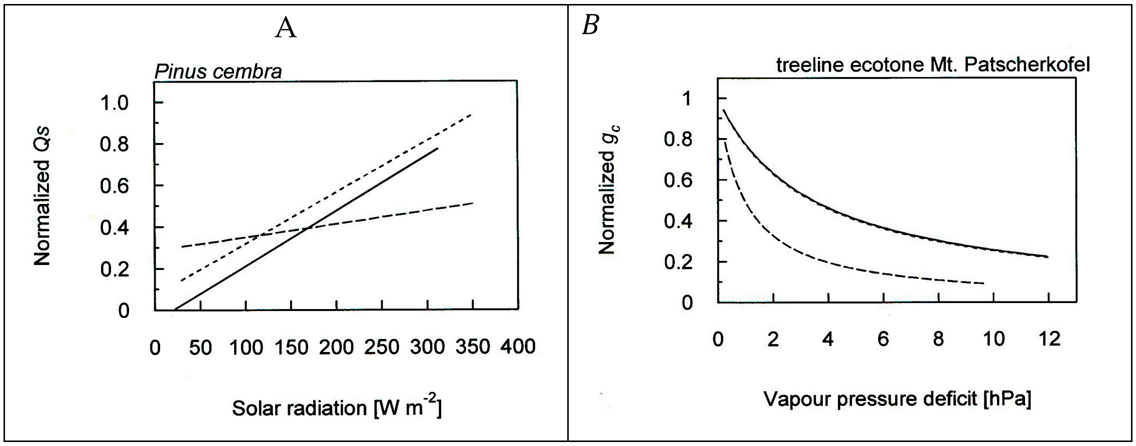

Figure 3. The relationship between (**A**) solar radiation and daily mean normalized sap flow density (Qs) and (**B**) between vapor pressure deficit and normalized daily mean crown conductance (g_c) of *Pinus cembra* at the krummholz limit (dashed lines), the treeline (dotted lines), and the forest limit (solid lines). After [98].

Soil temperature also seemed to control the water transport along the soil–plant–atmosphere continuum. Passive soil warming significantly improved sap flow density of *P. cembra* by 11% to 19% above the level of control trees during the second and the third year of treatment, respectively [38]. This effect appeared to result from a warming-induced reduction in water viscosity, an increased permeability of root membranes [101–103], and aquaporin-mediated changes in root conductivity [104,105], as tree fine-root production and mycorrhization did not respond to warming [106]. Hardly affected were leaf-level transpiration and conductance for water vapor, thus water-use efficiency stayed unchanged, as confirmed by needle $^{\delta13}C$ analysis [38].

Nevertheless, presuming a future environment with higher temperatures coupled with a decline in relative humidity and thus a considerable increase in evaporative demand [45] may reduce the water supply of trees at wind-exposed ridges and windward sun-exposed slopes with thin soil layers, particularly at their upper distribution limit. The latter is already affected today by temporary top-soil drought [52,98]. However, experimental studies on the effects of top-soil drought indicated that three years of rain exclusion did not considerably reduce sap flow density of *P. abies* and *L. decidua* saplings at the treeline in the Stubai Valley. The lack of a significant sap flow–soil water content correlation in both tree species indicated sufficient water supply, suggesting that whole tree water loss of young trees at the treeline primarily depends on evaporative demand [40]. Furthermore, roots of the treeline-associated conifers are able to penetrate into rocky undergrounds, allowing for the utilization of water sources in deep and wet soil layers, as shown for *L. decidua* trees using hydrogen stable isotope analysis [107].

4.2. Carbon Relations

Trees at the treeline do not show signs of greater limitations in net CO_2 uptake rate compared to trees at lower elevations [8], and their maximum net CO_2 uptake rate at ambient CO_2 is similar or even higher compared to their relatives at lower elevation sites [7]. As shown for current-year *P. cembra* needles in Figure 4, the temperature optimum of net CO_2 uptake shifted towards lower temperatures with increasing elevation, while maximum net CO_2 uptake rate at ambient CO_2 (A_{max}) tended to increase with elevation. The higher efficiency of carbon uptake per unit leaf area at the krummholz limit as compared to the treeline and the forest limit (Figure 4) may be attributed to elevation related differences in needle morphology [32,49] with respect to 100-needle dry weight and specific leaf area (Table 3).

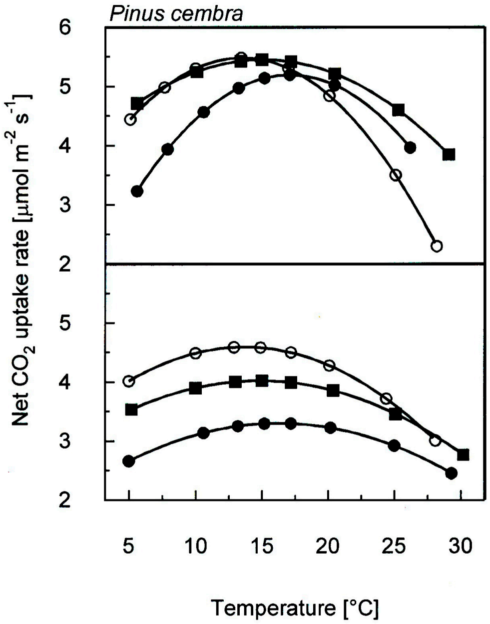

Figure 4. The relationship between temperature and net photosynthesis of fully developed, current-year *Pinus cembra* needles at the krummholz limit [open circles, tree line (closed squares), and the forest limit (solid circles) assessed in summer (top) and fall (bottom)]. After [48] and [108].

Table 3. The 100-needle dry weight and the specific leaf area (SLA) of current-year *Pinus cembra* needles at the krummholz limit (2180 m a.s.l.), the treeline (2100 m a.s.l.), and the forest limit (1950 m a.s.l.) on Mount Patscherkofel. After [108].

Elevation (m)	100-needle dry weight (g)	SLA (cm^2 g^{-1})
2180	1.04 ± 0.97	36.5 ± 1.0
2100	1.31 ± 0.72	35.4 ± 0.8
1950	1.29 ± 0.67	43.8 ± 0.7

Conversely, *P. cembra* needles did not show elevational differences in foliar nitrogen concentration [32]. Thus, the combination of high nitrogen content with low specific leaf area [considered as a morphological feature of sun type needles (≈thicker needles)] may enlarge the quantity of photosynthetic enzymes with increasing elevation. For plants in marginal habitats where assimilation is restricted to a short growing season, a higher amount of photosynthetic enzymes is suggested to provide a highly cost-effective system [109].

In general, air temperature hardly limits net CO_2 uptake, as more than 80% of full photosynthetic capacity is reached between 5 and 20 °C (Figure 4). During the growing season, net CO_2 uptake is primarily restricted by low irradiance and the accompanied low air and needle temperatures. Thus, the temperature optimum of net photosynthesis shifts towards higher values when photon flux density is high and towards lower values when photon flux density is low [110–112].

Dark respiration also adapts to the average temperature conditions that prevail in a local habitat. It is well known that, at any given temperature, trees growing at low temperature respire at higher rates as compared to trees growing in a warmer environment. When accounting for actual in situ temperatures, respiratory carbon losses of trees in the krummholz belt are similar or even lower than at the forest limit ([108]; Table 4). This genotypic and acclimative adaptation to lower temperatures [113,114] is also mirrored in a higher temperature sensitivity with increasing elevation (Figure 4, Table 4), permitting a higher metabolic activity at cooler conditions.

Table 4. Average air temperature during summer (T_{air}), corresponding night-time dark respiration (R_d), and the temperature sensitivity of respiration (Q_{10}) of current-year *Pinus cembra* needles at the krummholz limit (2180 m a.s.l.), the treeline (2100 m a.s.l.), and the forest limit (1950 m a.s.l.) assessed at the prevailing temperature conditions in summer 2007 on Mount Patscherkofel. After [108].

Elevation (m)	Tair (°C)	R_d (µmol m^{-2} s^{-1})	Q_{10}
2175	9.1	0.27	2.5
2100	10.0	0.28	2.3
1950	11.1	0.31	2.0

4.3. Long Term Trends in Carbon and Water Relations

At the treeline in the Central Austrian Alps, the maximum net CO_2 uptake rate at ambient CO_2 (A_{max}) of sun-exposed twigs from the upper canopy of mature, field grown *P. cembra*, *P. abies,* and *L. decidua* trees increased significantly between 1934 and 2012 (Figure 5). Temporal changes in A_{max} of *P. cembra* were also mirrored in tree growth and tree-ring $\delta^{13}C$, as basal area increment was significantly positively correlated with increasing A_{max}, whereas tree-ring $\delta^{13}C$ was significantly negatively correlated with A_{max}. Furthermore, in *P. cembra,* A_{max} tended to increase with tree-ring derived intrinsic water-use efficiency (Figure 5) and hence also with tree-ring derived intercellular CO_2 partial pressure, similar to a classical A/Ci curve [45]. The observed increase in A_{max} of *P. cembra* can be ascribed to both a rise in atmospheric CO_2 concentration and to the observed increase in T_{air}. In addition, temperature optimum of A_{max} for *P. cembra* increased from 12.5 °C in 1956 [111] to 17.1 °C in 2007 [48]. Thus, the observed increase in temperature optimum of A_{max} of 4.6 °C during the period 1956–2007 matched the observed increase in mean growing season air temperature of 0.9 °C per decade. In parallel to A_{max}, transpiration of *P. cembra* increased from 0.42 mmol m^{-2} s^{-1} in 1934 [115] to 1.12 mmol m^{-2} s^{-1} in 2012 [38]. As a result, the instantaneous water use efficiency of photosynthesis did not change considerably and averaged 4.3 ± 0.7 µmol mol^{-1} between 1934 and 2012, suggesting an increase in stomatal conductance for water vapor during the past 89 years [45]. Temporal patterns in $\Delta^{13}C$ and $\Delta^{18}O$ also suggest a parallel increase in CO_2-fixation and stomatal conductance of conifers at the treeline during the past 40 years [42]. The stability in tree-ring derived instantaneous water-use efficiency of 70-year-old *P. cembra, P. abies,* and *L. decidu*a trees was accompanied by an increase in basal area increment, suggesting that young trees benefit from both climate warming and rising ambient CO_2 [42]. To the contrary, in 120-year-old *P. cembra* trees, nearby basal area increment remained largely stable during the past 35 years, indicating that trees had matured after 95 years of growth [45]. Thus, it seems that in environments under non-limiting water availability, as is the case at the treeline in the Central Austrian Alps [44], increasing temperature counteracts the diminishing effects of rising atmospheric CO_2 concentration on leaf conductance in adult trees [116,117].

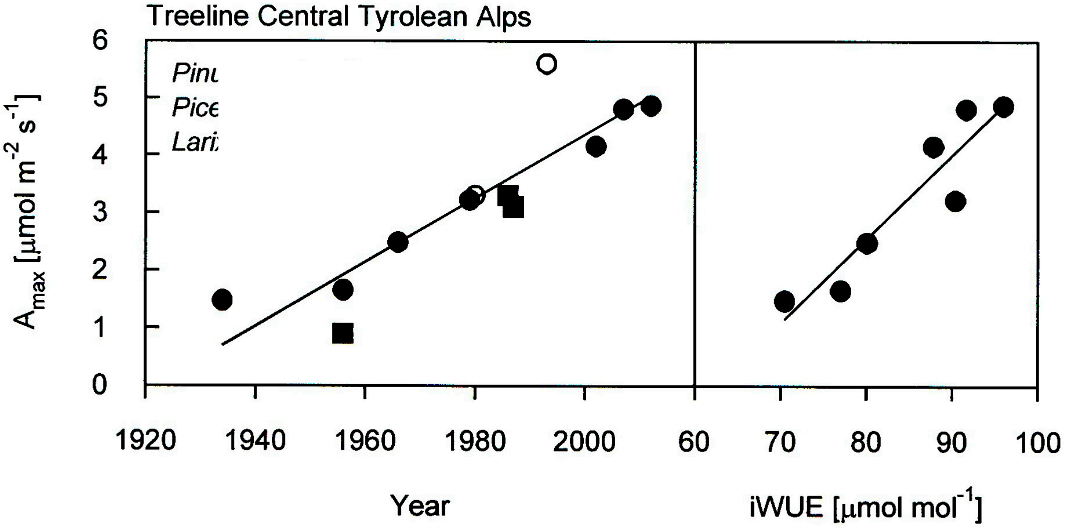

Figure 5. Temporal variation in maximum net CO_2 uptake rate at ambient CO_2 (A_{max}) of *Pinus cembra* (solid circles), *Picea abies* (solid squares), and *Larix decidua* (open circles) between 1925 and 2013 (left), and the relationship between A_{max} and tree-ring derived intrinsic water-use efficiency (iWUE) obtained for *Pinus cembra* at the treeline in the Central Tyrolean Alps. Compiled after [38,45,48,110,115,118–124].

5. Treeline Fluctuations

Radiocarbon dating of soil charcoal fragments indicates that the treeline has changed its position during the Holocene several times due to anthropogenic impacts [125]. In the Central Alps, the treeline reached its maximum elevation of 2700 m a.s.l. between 8000 and 5000 years BP [126,127]. Humans have influenced the timberline ecotone of the Tyrolean Alps since 7000 years BP [128–130], as nearly all accessible slopes were deforested to gain pastures [131] and timber for mining, firewood, and construction wood, particularly during the Middle Ages [21]. Presently, the actual treeline in the Central Tyrolean Alps is 150–300 m below its potential climatic maximum reached during the Holocene [132,133]. On siliceous parent material, the presence of Podzols under dwarf shrub communities above the present forest limit points towards the existence of a forest canopy in the past [134]. Nevertheless, topography and local climate have influenced human impacts; in particular, slopes with southern exposure became completely deforested [125]. Therefore, it is uncertain if the present actual treeline in the Central Tyrolean Alps mirrors equilibrium between climate and tree-specific ecophysiological features [25]. Furthermore, potential changes in ecosystem dynamics and functioning have also been attributed to recent changes in land-use management [135].

As growth [50] and reproduction [5,86,136] of trees at the treeline are controlled by temperature, an upslope migration of tree species has been predicted under climate warming ([21] and further references therein). Yet, the elevational movement of timberlines is dependent initially on new seedling establishment in favorable microsites that appear to be generated by ecological facilitation [86]. Even so, treelines influenced by pastoral use for centuries, as in the Central Austrian Alps, for example, respond differently to climate warming than undisturbed treelines [21]. Thus, the observed increase in seedling establishment in potential habitats beyond the forest limit of the

Central Tyrolean Alps [132,133] is probably a consequence of decreasing grazing pressure [24] and changes in land-use management.

A huge percentage of seedling re-establishment at the treeline in the Swiss Alps [137] also resulted from invasion into potential habitats rather than an upward migration, as shown in pine seedlings by [70] and [138], leading [11] to suppose that the treeline in the Central European Alps behaves in a "conservative" way. Nevertheless, tree advancement to higher elevations is primarily dependent on seedling establishment in favorable microsites [86]. In addition, seedlings have to cope with a dense dwarf shrub and/or a closed grass cover and thus with impoverished mycorrhizal symbiosis; consequently, they also encounter competition for below-ground resources. Treeline migrations, however, may also influence carbon metabolism, soil microbial activity, and even ecosystem fluxes within the treeline ecotone ([18] and further references therein). Thus, understanding seedling physiology is a prerequisite for estimating future elevational shifts in treeline associated conifers within the Central Tyrolean Alps.

6. Conclusions and Climate Change Perspectives

Changes in temperature and soil water availability as well as the increasing atmospheric CO_2 concentration interact in complex ways in trees and forests at the treeline. As trees within the treeline ecotone are not carbon limited [8,13], climate warming—rather than the rising atmospheric CO_2 level—causes alterations in the ecological functioning of the treeline ecotone in the Central Austrian Alps [10,18]. Additional carbon acquired by treeline trees upon warming is available for both below (water nutrients) and above (light) demands with respect to resource sequestration [139] and competitiveness. The latter is known to curtail tree survival at the treeline [140]. Although the water uptake from soils will be improved by further climate warming due to an increased permeability of root membranes and aquaporin-mediated changes in root conductivity, the water balance may be perturbed at wind and sun-exposed sites with shallow soils due to increasing evaporative demand, as is indicated already today in the krummholz zone [98].

One has to take into account that treelines are vulnerable to anthropogenic influences such as land use changes and management practices [135]. The current observed seedling re-establishment at the treeline in the Central European Alps is an invasion into potential habitats due to decreasing grazing pressure rather than an upward-migration [133,137]. This kind of habitat reoccupation suggests the treeline in the Central European Alps behaves in a conservative way [11].

Moreover, in a future, warmer environment, tree population dynamics within the treeline ecotone will be controlled by severe weather events such as early and late frost events or soil drought during the summer rather than by a gradual increase in mean surface temperature [141]. Finally, seedling establishment should be considered for understanding the altitude of the treeline [86]. However, as there is a lack of knowledge in this particular topic within the treeline ecotone in the Central Austrian Alps, further research is needed regarding the importance of this life stage for evaluating treeline shifts and limits in a future, changing environment.

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