

Tree Growth near Treeline: Abrupt or Gradual Reduction with Altitude?

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Abstract

Natural climatic treelines are relatively discrete boundaries in the landscape established at a certain elevation within an otherwise continuous gradient of environmental change. By studying tree rings along elevational transects at and below the upper treeline in the European Alps, we (1) determine whether radial stem growth declines abruptly or gradually, and (2) test climatic influences on trees near treeline by investigating transects for climatically different historical periods. While tree height decreases gradually toward the treeline, there is no such general trend for radial tree growth. We found rather abrupt changes which imply threshold effects of temperature which moved upslope in a wave-like manner as temperatures increased over the past 150 yr. Currently radial tree growth at treeline in the Alps is the same magnitude as at several hundred meters below current treeline. Over short intervals, tree-ring width is more dependent on interannual climatic variability than on altitudinal distance to treeline. We conclude that (1) the elevational response of tree-rings includes a threshold component (a minimal seasonal temperature) and that (2) radial growth is more strongly correlated with year to year variation in climate than with treeline elevation as such. Our data indicate that the current treeline position reflects influences of past climates and not the current climate.

Introduction

Climatic high-elevation treelines are conspicuous vegetation boundaries that occur over a wide range of latitudes. Highest treeline positions (>4000 m) are found in subtropical mountains of the northern hemisphere. At high latitudes, the elevational "alpine" treeline merges with the low-altitude arctic treeline. Regionally a maritime climate can suppress treelines and a continental climate can facilitate higher treeline elevations (the so-called "Massenerhebungseffekt," Brockmann-Jerosch, 1919).

Many explanations for the treeline phenomenon have been attempted in the past (e.g., Däniker, 1923; Tranquillini, 1979; Körner, 1998). Some correlative approximations such as the 10°C isotherm of the warmest month have been found to have predictive value on a local but not on a global scale. A worldwide consideration of treeline positions does not support the usefulness of notions such as "treeline is a complex phenomenon and results from interactions of many different (!) environmental drivers" (Körner, 1998). If this were true, natural alpine treeline positions would not correlate with *one* specific component of the mountain climate across the globe, which they do (e.g., seasonal mean temperatures of 5 to 7°C, Körner, 1998 and unpublished data). Many phenomena (photosynthesis, winter water relations, branch maturation, snow and ice injury, seedling survival), which may be of local importance for treeline formation, are less significant on a global scale.

Across the treeline ecotone, which is the transition from tall closed forest "timberline" to the upper limit of the "krummholz" belt, stand density and tree vitality decreases rapidly with increasing elevation. The response of the radial growth of trees across a 250-m elevational gradient within the treeline ecotone of central Europe is the focus of the present study. Following suggestions by Däniker (1923), we explore elevational trends in

radial growth in order to understand the upper limits of tree distribution.

The slowing of tree growth within the treeline ecotone is a well acknowledged phenomenon in the forest literature (e.g. Ott, 1978). But a systematic quantitative assessment has not yet been considered. Is the climatic boundary of tree distribution associated with a tree-ring width of zero? In a study of birch in Scandinavia, the successful extrapolation of a linear elevational decrease of tree-ring width within the upper 100 m of the ecotone seemed to support this hypothesis (Treter, 1984). How and why does the vigor of healthy and undamaged trees decline so rapidly as one approaches the climatic tree limit?

Because mean air temperature during the growing period decreases by ca. 0.6 K per 100 m elevation, a reduction of tree-ring width towards treeline may be interpreted as a direct reaction to decreasing temperature. In contrast, variation in ring width in trees at equal elevational distance from the treeline between different years or decades can be assumed to reflect climatic variation. The reconstruction of past climates from tree rings is a major topic in dendrochronology (e.g., Briffa et al., 1990; Schweingruber et al., 1991), but not the aim of the present study. Instead, we were interested in the growth response itself.

Our analytical approach used a curvature analysis of the elevational decline of tree-ring width in the uppermost zone of tree growth. We expected "initial slope" and "sharpness" of curvature (decline of ring width with elevation) near treeline to provide a "fingerprint" of the current and past dependence of tree growth on climate. The elevational response may be a linear or nonlinear decline, or its shape may vary over the years, depending on concurrent climate.

We intend to deduce early signals of a potential advance or retreat of high elevation forest boundaries from growth dynamics of mature trees within the ecotone, rather than from actual recruitment success beyond the current limit. We believe that seed-

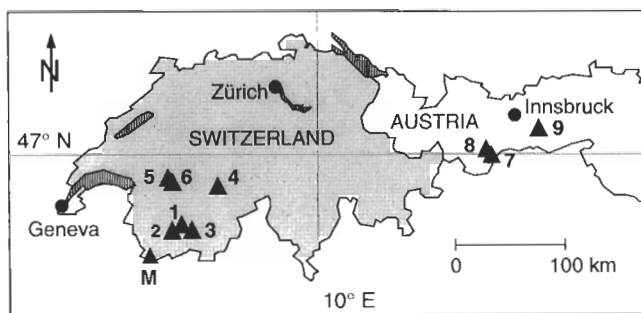


FIGURE 1. Sampling locations in the Swiss and Austrian Alps (central Europe). Site numbers, latitudes, and longitudes are listed in Table 1.

ling success has low predictive value as long as individuals are small and nested in the aerodynamic boundary of low-stature vegetation (Körner, 1998).

Methods

DEFINITIONS

For practical reasons, in this analysis a *tree* is defined as an upright woody plant with a single above-ground stem that reaches a height of at least 3 m, independently of whether reproduction occurs or not. This height assures that such a tree would have its crown closely coupled to prevailing atmospheric conditions and protrudes above deep snow where snow occurs.

The definition of an upper boundary of tree occurrence is more delicate, because such a line refers to the boundary of a vegetation type and, as formulated so elegantly by Armand (1992), "any natural boundary is in reality a transition zone, which has its own two boundaries. They are, in turn, also transition zones with their own boundaries, and so on endless. So localisation of a natural border is in principle inexact and therefore determined by convention."

Tree height decreases continuously with elevation at all locations. The uppermost individuals are shrub-like. For practical reasons, we have chosen the position of the uppermost trees (≥ 3 m) as the upper end of the sampling transects. This elevation is

referred to by the term *outpost treeline* because these trees were often, but not always, isolated "outposts." This simply turned out to be the most useful and practical convention for this analysis. All calculations and analyses refer to this elevation as the (theoretical) point of minimum growth. Since these outposts hardly ever exactly met our "3-m-tree" criterion, the actual zero-point of our transects was obtained by linear interpolation of tree heights. At all transects, this point differed very little (less than 20 m of elevation) from the position of the uppermost >3 -m outpost tree.

The *treeline* marks a line connecting the highest patches of forest within a given slope or series of slopes of similar exposure. This definition corresponds to the one used by Brockmann-Jerosch (1919) and Däniker (1923) in their classical monographs on treeline biology of the Alps. At our sampling sites the treeline is roughly 50 m below the outpost treeline. We refrain from using "timberline" in this study, which would refer to the upper limit of closed forest.

Tree age is always the age of the pith of the tree at our coring height (50 to 80 cm above the ground). If the pith was missed only slightly (as easily happens with cores in asymmetric or large trees) the number of missing tree-rings was calculated from the diameter of the innermost intact tree-ring and the average width of the 5 following rings. If the pith was missed by more than 4 cm or if the tree was hollow, the absolute tree pith age remained unknown. The sampled trees may well be 30 yr (or more) older than the pith hit by the core because it may take a tree 30 or more years to attain a height of 80 cm at such high elevations. So the true absolute age counted from the year of germination can not be obtained without felling the tree, but this problem should not affect our analysis in a systematic way.

SITE AND TREE SELECTION AND DATA COLLECTION

Cores were collected along straight elevational transects from the uppermost outpost tree downwards across the treeline ecotone (Fig. 1, Table 1) at each of nine locations in the Swiss and Austrian Alps. We avoided areas of obvious human influence on treeline position or abrupt changes in slope or soil properties. At all sampling locations the tree height continuously decreased with increasing elevation. At each location, we sampled

TABLE 1
Coring sites (for site numbers see Fig. 1)

	Site no.	Aspect	Latitude	Longitude	Elevation of outpost treeline (m) ^a	Dominant species ^b	Number of sampled trees	Mean tree-ring width ^c
Marenda, CH-VS	1	N	46° 12' N	7° 30' E	2370 m	<i>Pinus</i>	79	1.41 mm
T. d. Bonvin, CH-VS	2	SSE	46° 12' N	7° 30' E	2380 m	<i>Pinus</i>	28	1.13 mm
Mont Noble, CH-VS	3	E	46° 12' N	7° 30' E	2510 m	<i>Pinus</i>	27	0.97 mm
Elsigen, CH-BE	4	SW	46° 32' N	7° 38' E	2100 m	<i>Picea</i>	14	1.00 mm
Les Mosses I, CH-VD	5	S	46° 23' N	7° 08' E	2050 m	<i>Picea</i>	10	1.01 mm
Les Mosses II, CH-VD	6	N	46° 23' N	7° 08' E	2050 m	<i>Picea</i>	11	1.06 mm
Obergurgl, A-TI	7	ENE	46° 50' N	11° 01' E	2320 m	<i>Pinus</i>	20	1.18 mm
Poschach, A-TI	8	NW	46° 54' N	11° 03' E	2140 m	<i>Pinus</i>	10	2.19 mm
Glungezer, A-TI	9	NW	47° 20' N	11° 30' E	2150 m	<i>Pinus</i>	15	1.14 mm
Gd. St-Bernard ^d	M		45° 52' N	7° 10' E	2480 m	Alpine climate station		

^a Elevation of outpost treeline: elevation where uppermost >3 m tall trees occur.

^b *Pinus* = *Pinus cembra* (cembran pine), *Picea* = *Picea abies* (Norway spruce).

^c Mean of all tree-rings older than 20 yr from all sampled trees 50–150 m below outpost tree line.

^d Grand St. Bernard = alpine station of the Swiss Meteorological Institute (SMI). CH: Switzerland, VS: Canton of Valais, BE: Bern, VD: Vaud; A: Austria, TI: Land Tirol.

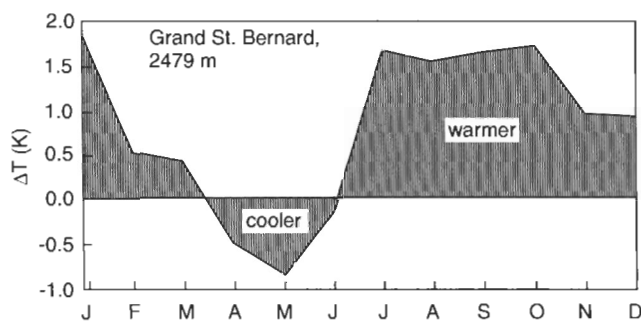


FIGURE 2. Deviation of the mean monthly air temperatures of 1968–1997 from 1820–1849 at Grand St. Bernard (2479 m, 200 m above outpost treeline).

dominant trees along one discrete transect. Only undamaged and undeformed trees were considered.

Tree elevation was determined by an atmospheric pressure altimeter, which was calibrated several times per day with topographic maps 1:25,000 (contour interval 20 m). Tree heights were estimated by eye. Cores were taken with a 5-mm increment borer at 50–80 cm height, parallel to the slope contour, thus minimising the influence of compression wood. Ring width (± 0.01 mm) was measured and recorded with an electronic analysis bench (LINTAB, TSAP, Heidelberg, Germany) and a microscope.

Climatic data were taken from Grand St. Bernard Station, the only alpine station of the Swiss Meteorological Institute (SMI) which provides monthly mean air temperatures since 1818 (Fig. 2). The station is situated at 2479 m a.s.l., approximately 200 m above the “outpost treeline” and at 60 to 80 km distance from the Swiss coring sites.

DATA ANALYSIS AND STATISTICAL APPROACH

In the following we describe how we standardized the raw data obtained from wood cores for differences in tree age, absolute elevation of outpost treeline and region specific tree vigor. For the sake of comparability across locations, we first calculated a transect-specific “reference ring width” which equalled the mean of all tree rings between 20 and 200 yr of age for all trees sampled over the range of 50 to 150 m below the “outpost treeline” (i.e., excluding the uppermost trees; Table 1, right column). This mean tree-ring width provides a transect-specific reference (= 100%) of tree vigor. Individual tree-ring data from different elevations at each site were then expressed relative to this reference. Given the steep slopes, which induce asymmetric compression wood, and the often irregular cross-sectional shape of trunks, basal area increments would not yield a more reliable approximation of tree growth. It would rather introduce further assumptions, with the large differences in height growth still unaccounted for. The same basal area increment could be found in trees of 3 and 15 m height. For the basal area to become a better approximation of tree growth, similar tree height and branchingness are prerequisites not met across our transects.

Tree-rings from periods during which a given tree was younger than 20 yr (pith age) were excluded from the analysis, because we were not interested in responses of such small trees. Tree-age effects for trees between 20 and 110 yr of pith age were accounted for by detrending the raw data with the following cubic polynomial function (fitted to the bulk of tree-ring data for all locations):

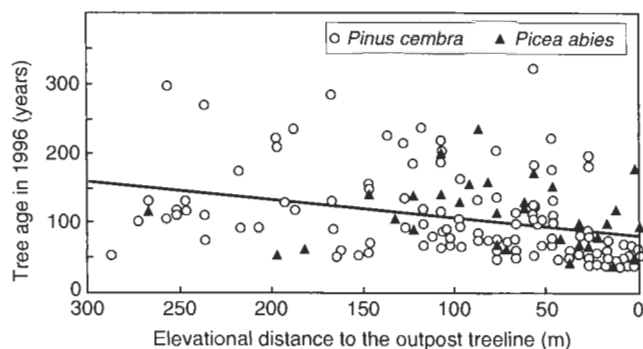


FIGURE 3. Age distribution of dominant trees by altitudinal distance to the outpost treeline. Linear regression: tree age = $81.2 + 0.28$ (distance to outpost treeline), $r = 0.33$. Tree age is the age of the tree pith at coring height (50 to 80 cm above ground). There is no significant difference in the age distribution between the two tree species.

$$\text{ring width}' = \text{ring width}/0.89 + 0.02659 \cdot \text{age} - 0.00046 \cdot (\text{age})^2 + 0.0000020 \cdot (\text{age})^3; \quad 20 < \text{age} \leq 110.$$

There was no need to apply such age-trend correction for tree-ring pith ages older than 110 yr, because our data did not exhibit any width-age correlation for this age class.

The elevation of the treeline at the different sites varied between 1950 and 2350 m, the uppermost tree outposts were found between 2030 and 2510 m (Table 1). Throughout this paper, the elevation of individual trees is always expressed as the altitudinal distance to the respective “outpost treeline” (see above) and not in meters above sea level. Thus, a tree with an “outpost treeline distance” of 80 m is situated 80 m below the outpost treeline, irrespective of the topographical elevation of its location.

In all transects, the forests were dominated by only one tree species. Either cembran pine (*Pinus cembra*) or Norway spruce (*Picea abies*) covered at least 90% of the respective stands. We found no tree species-specific influence on detrended ring widths (*t*-test with log-transformed data, which were normal-distributed), therefore we decided to pool the data for *Pinus cembra* and *Picea abies* (Fig. 3).

Ideally one would like to have all age classes similarly represented during all historic periods in all transects. However, many of the large, old cembran pines we cored (diameter >40 cm) were hollow, hence we do not know their absolute age and we miss tree rings from their early growth phase. The resultant skewed age representation of our data set constrained the number of records for the first part of the 19th century. This may cause tests for effects of historic climate trends on tree growth to be confounded with tree age.

Results

TREE AGE

The closer trees were situated to the outpost treeline the more the age of the sampled, dominant trees decreased (Fig. 3). However, with reference to our 50- to 80-cm coring height, we found 100-yr-old or older nonhollow trees within the uppermost 50 m of the ecotone at all sampling locations. Even 200-yr-old individuals (pith age at coring position) were found 50 m below the present “outpost treeline” (roughly corresponding to the current treeline). If one accounts for the years elapsed between tree

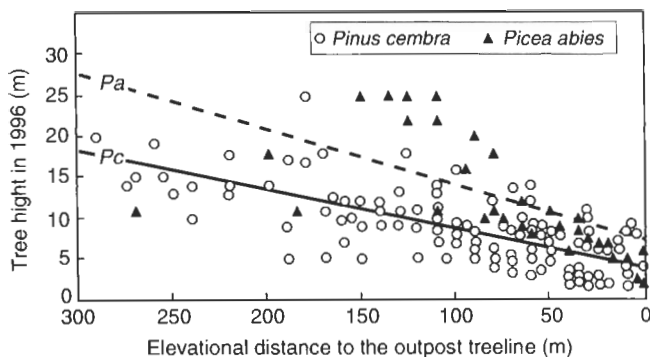


FIGURE 4. The height of dominant trees across the treeline ecotone. Linear regressions: *Picea abies* (Pa, dashed line): tree height = $6.4 + 0.072$ (distance to outpost treeline), $r = 0.64$; *Pinus cembra* (Pc, bold line): tree height = $4.0 + 0.046$ (distance to outpost treeline), $r = 0.69$.

germination and our coring height, this indicates that there was no major shift in treeline elevation within the last ca. 250 yr.

TREE HEIGHT

Tree height of dominant trees decreases as one approaches the outpost treeline (Fig. 4). With an error probability of $<10^{-4}$ (one-way ANOVA) this effect cannot be attributed to the somewhat lower age of trees at outpost treeline only, that is, trees in the upper zone are not just smaller because they are younger. The reduction of tree height with increasing elevation was site-specific and varied between 2 and 17 m per 100 m of elevation. At a given tree age and position in the ecotone, *Picea abies* is significantly taller than *Pinus cembra* (Fig. 4).

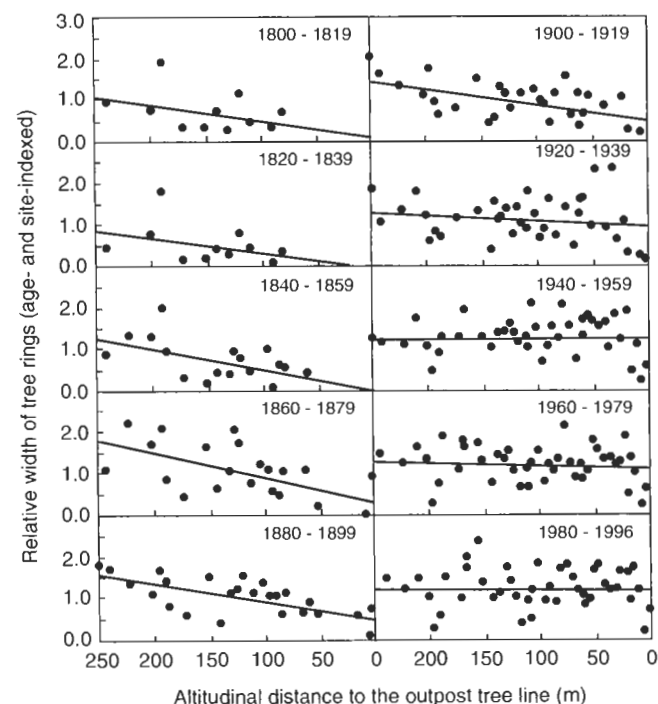


FIGURE 5. Radial stem increment in relation to time period and altitudinal distance to the outpost treeline. Each point is the mean value of all age detrended ring width data of all trees at the same distance to outpost treeline. For slopes, intercepts and correlation coefficients of regression lines see Table 2.

TABLE 2

Ringwidth reduction with increasing elevation in the treeline ecotone at different historical periods

Historical time period	r	Tree-ring decrement per 100 m elevation (mm)	Tree-ring width at outpost treeline elevation (mm)
1800–1819	0.40	0.39	0.12
1820–1839	0.38	0.37	0.00
1840–1859	0.61	0.49	0.08
1860–1879	0.57	0.59	0.38
1880–1899	0.68	0.45	0.50
1900–1919	0.57	0.37	0.53
1920–1939	0.18	0.14	0.98
1940–1959	0.01	0.00	1.28
1960–1979	0.12	0.08	1.12
1980–1996	0.00	0.00	1.22

HISTORICAL TRENDS

There is no difference in tree-ring width between *Picea* and *Pinus* (one-way ANOVA) but a distinct historical trend exists in the uppermost 250 m of the treeline ecotone. In the first part of the 19th century, annual increments linearly decreased with increasing elevation. After 1940, average tree-ring width within the uppermost 250 m below the outpost treeline was similar, irrespective of the elevation of the tree location. The time period between 1860 and 1920 represents a period of transition. At the lower end of the ecotone, 250 m below outpost treeline, mean ring widths have not changed since 1840 (Fig. 5, Table 2). Therefore, whether one detects a historical trend in tree-rings depends on the distance of the coring site to the outpost treeline.

The annual radial stem increment within the uppermost 100 m below outpost treeline did not increase continuously over the considered time period. The increase of tree-ring width occurred rather abruptly and with an elevation-specific time lag (Fig. 6). Within only 15 to 20 yr, average radial increment doubled from 0.4 mm to 0.8 mm yr^{-1} across sites. Since then, ring width has never fallen below these means. This phenomenon started around 1850 for trees 50 to 100 m below present outpost tree-line. Around 1870, it occurred for trees 30 to 50 m below the

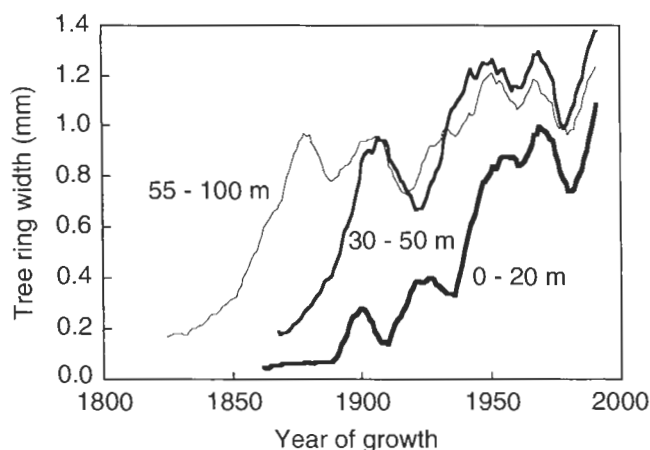


FIGURE 6. Radial tree stem increment (age detrended) of the past 170 yr in the uppermost zone of the treeline ecotone. The three lines represent tree rings from nine transects cored at three different ranges of elevational distance from the outpost treeline.

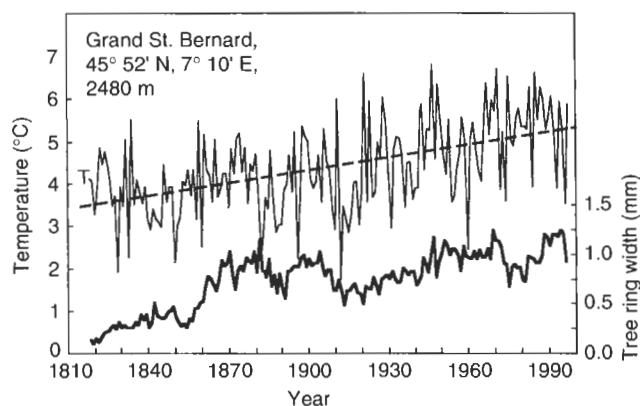


FIGURE 7. Mean monthly temperatures of the growing period (June–September) and mean, age-detrended ring width of trees 50 to 150 m below current outpost treeline of nine transects in the Central Alps. Temperature data: Grand St. Bernard Station 2479 m a.s.l. (200 m above outpost treeline). Regression of mean temperature with year: $r = 0.51$, slope = $0.0102^{\circ}\text{C yr}^{-1}$.

present outpost treeline, and for trees at present outpost treeline, the major increase is apparent after 1940.

Discussion

A recent stimulation of radial tree growth near cold climate treelines has been documented previously (e.g., Sonesson and Hoogsteeger, 1983; LaMarche et al., 1984; Cooper et al., 1986; Peterson et al., 1990a, 1990b; Innes, 1991; Petersson, 1994, 1998; Nicolussi, 1995; Weber, 1997).

Compared to the second half of the 19th century present mean temperatures represent a warming of 1.5 K for the growing period (June to September) at treeline elevations in the Alps (Fig. 2). However, this long-term trend is superimposed on more pronounced short-term fluctuations. At Grand St. Bernard Station (200 m above outpost treeline), within any period of 20 yr the coolest year was between 2.5 to 4.0 K cooler than the warmest. An extreme example is the growing seasons in 1911 and 1912, in which the mean temperature was 7.1°C in 1911, but only 2.9°C the following year (Fig. 7).

These interannual temperature fluctuations correspond to a difference in elevation of several hundred meters (e.g., $3\text{ K} / 0.6\text{ K } 100\text{ m}^{-1} = 500\text{ m}$). On the other hand, the elevational range across which radial tree growth rapidly declines within the ecotone is not wider than 100 m of elevation at all studied sites, which corresponds to a temperature difference of 0.6 K. This small difference (much smaller than interannual differences) suggests a signal that becomes critical for treeline formation only when integrated over many years.

A general warming of 1.5 K (which corresponds to 250 m of elevation) during the growing period since 1820 was measured at a meteorological station 200 m above climatic treeline (Grand St. Bernard, see Fig. 7). Tree-ring widths from our coring sites appear to reflect a warming in the upper treeline ecotone, but in a peculiar way (Figs. 5, 6). Currently, ring width at outpost treeline in the Alps is as wide as it was 250 m lower in the first part of the 19th century (Fig. 5). A 1.5 K warming is analogous to an ascent of treeline of ca. 250 m. Recent shifts of treeline have been suggested by several authors (e.g., Griggs, 1946; Innes, 1991). However, our data do not indicate a significant upslope migration over the last 180 yr, given the great abundance of 150- to 200-yr-old trees in the upper part of the ecotone. From the decrease of mean tree age with increasing elevation (slope

of the regression line in Fig. 3) of 0.28 meters of elevation per one year, a theoretical ascent of outpost treeline of only 50 m since 1820 could be assumed ($180\text{ yr} \times 0.28\text{ m a}^{-1}$). If there is an upslope move of the outpost treeline of 50 m and a warming of the growing period of 1.5 K since 1820, the mean air temperature at the outpost treeline during the growing period is theoretically 1.2 K higher than it was 180 yr ago (50 m of elevation correspond to 0.3 K). The observed "conservative" behavior of treeline elevation in the Alps is well evidenced for most of the Holocene (Burga, 1988). Similarly, Petersson (1998) reports changes in treeline elevation of less than 100 m over palaeoperiods differing by 2 to 3 K.

We dismiss the view that treeline formation is a question of seedling establishment, because almost everywhere seedlings may be found above outpost treeline (Wardle, 1971; Hättenschwiler and Körner, 1995; references in Körner, 1998). The mere existence of a krummholz belt illustrates that sporadic seedling establishment of woody plants is possible above treeline (except where fire is prohibitive, which is not the case at our sites). The critical phase for tree establishment is the stage when a young tree reaches a height where needles become closely coupled to the thermal and radiative conditions of the free atmosphere and do not continue to profit from radiative heating near the ground (Grace, 1990). An advance of treeline could take place only if a long-term warming trend stimulates growth frequently enough (also in cooler years), or, in other words, if low-temperature events/periods which limit growth are so rare that they are insignificant.

It is unknown whether enhanced nitrogen deposition contributes to tree stimulation at treeline. Our data do not support such a critical role of nutrients. According to our analysis, the growth increase in the Alps occurred with a systematic time-lag with increasing elevation. A difference in elevation of 50 m (corresponding to a horizontal distance of ca. 100 m) corresponds to a time-lag of 20 to 30 yr (Fig. 6). However, increased nutrient input is uniform over large areas (Gäggeler, 1997) and, thus, the observed dramatic changes in growth cannot be explained by a nutrient effect. Time-series analysis also led Nicolussi et al. (1995) to conclude that high-elevation trends in tree-ring width do not match nitrogen input dynamics of the 20th century in the Alps. Similarly such a threshold response of tree growth which is delayed with elevation does not strongly favour a stimulation of tree growth by atmospheric CO_2 -enrichment alone. During the years when this upslope wave of growth stimulation occurred (in the 2nd half of the 19th century, see Fig. 6), CO_2 -enrichment was minute. It has been explained elsewhere (see discussion in Körner 1998) that it is unlikely that treeline trees have a carbon balance problem. They rather have a carbon investment problem associated with periodically low temperatures.

If temperature dominates growth responses of trees near treeline, our data suggest that growth-limiting threshold temperatures for shoot or root meristems exist, because the stimulation of radial growth exceeds rates of any known proportional metabolic temperature response. Radial growth responses that occurred over the past 150 yr may reflect the operation of a "critical" temperature, above which responses are less temperature sensitive. It remains to be resolved whether seasonal means, temperature sums above certain thresholds or other measures of direct or indirect temperature influences on meristems provide the best explanation.

The highest correlation between tree-ring width and monthly or seasonal mean air temperatures from a meteorological station was $r = 0.52$ (mean temperature of July). Remarkably, Peterson (1998) also found the best correlation (ca. 0.5) with sum-

mer temperature in high-elevation forests in the Olympic Mountains of western North America. This supports the view that temperature is the major driver of radial stem increment, but the way this signal is integrated over very long periods is not well understood and predictions for shorter periods seem to be very unprecise. During some periods the direction of trends in air temperature at Grand St. Bernard and radial stem increment near treeline were even opposite (Fig. 7, e.g., 1857–1863, 1985–1992). The period of increased growth between 1855 and 1870 is not reflected in the air temperature data, and tree ring width between 1912 and 1920 was more than twice as great as between 1840 and 1850, although both periods exhibited the same temperature sum during the growing period. We do not understand why the observed growth increase is delayed with increasing elevation (Fig. 6) and why a difference of 50 m elevation corresponds to a delay of 25 yr. A narrow threshold temperature for growth-related processes appears to be most plausible. Factors other than temperature such as local soil moisture or nutrition are unlikely causes of the general growth increase, because growth was measured at so many locations with different local hydrology across the Alps (cf., Kienast et al., 1987).

Individual trees appear to respond very sensitively to temperature, but treeline does not. Sub- and supraoptimal years affect growth, but do not influence treeline position, except if they persist over very long periods of time (Peterson, 1998). Currently, there are no trees in the Alps at elevations high enough where the temperature would limit radial tree growth to near zero increments. In order to detect early indications of treeline responses to global warming, the study of growth dynamics within the treeline ecotone, rather than at its upper boundaries (Slatyer and Noble, 1992), appears most promising.

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