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Effects of microsite on growth of *Pinus cembra* in the subalpine zone of the Austrian Alps

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Abstract – We examined growth in *Pinus cembra* L. (28 years old) across the treeline ecotone from 1900 to 2100 m elevation in the Alps. Eighteen plots were chosen at different microsities which are defined as a combination of elevation and steepness (gentle vs. steep slope) on a south-facing slope in the Schmirn Valley, Tyrol/Austria. Over the range of altitudes studied, elevation and steepness had influences on growth depending on tree size: (1) Elevation and steepness had little effect on growth as long as trees were very small (< 0.5 m in height); (2) Both elevation and steepness affected tree growth significantly when the tree height was between 0.5 and 3 m; (3) As trees exceeded 3 m in height, tree canopies fully covered the ground surface and created a forest microclimate causing growth to decline with increasing elevation, irrespective of steepness. We conclude that the microsite related to microclimate, controls growth during the early life stages of trees, but following canopy closure the local climate (mesoclimate) associated with topography begins to determine tree growth.

growth responses / high altitude / micro-environmental conditions / tree ecology / treeline ecotone

Résumé – Effets de la microstation sur la croissance de *Pinus cembra* dans la zone subalpine des Alpes autrichiennes. Nous avons examiné la croissance de *Pinus cembra* L. (28 ans) dans l'écotone de la limite forestière entre 1900 et 2100 m d'altitude dans les Alpes. Dix-huit placettes ont été choisies dans différentes microstations définies selon l'altitude et la déclivité du terrain sur une pente exposée au sud dans la vallée de Schmirn, dans le Tyrol autrichien. Dans toute la zone étudiée, l'altitude et la déclivité ont exercé une influence qui dépendait de la taille de l'arbre: (1) elles avaient peu d'effet sur la croissance des arbres de très petite taille (< 0.5 m de haut); (2) elles avaient un effet significatif sur les arbres d'une hauteur entre 0,5 et 3 m; (3) à partir de 3 m de haut, la canopée couvrait complètement la surface du sol et créait ainsi un microclimat forestier qui entraîne un ralentissement de la croissance avec l'augmentation de l'altitude, indépendamment de la déclivité. Nous en concluons que la microstation liée au microclimat détermine la croissance des arbres durant leur jeune âge, mais après la fermeture de la canopée, le climat local (mésoclimat) associé à la topographie commence à influencer la croissance des arbres.

réactions à la croissance / altitude / conditions microenvironnementales / écologie des arbres / écotone de la limite forestière

1. INTRODUCTION

Cembra pine (*Pinus cembra* L.) is an important species of forests in the subalpine zone of the Alps, where forests have been depressed from the natural climatic treeline by land use over several centuries [22, 24, 36]. As a consequence avalanche risk has enhanced. Hence, programs of forest restoration have been initiated in the Alps several decades ago, to prevent and avoid such damages. The objective of this study addressed to a better understanding of tree growth in this area.

The slower growth rate of subalpine trees is a documented phenomenon in forestry literature. Many authors have given a common description of decreasing growth of subalpine trees with increasing elevation (e.g. [5, 15, 16, 18, 19, 28, 37]). In

the Swiss and Austrian Alps, the reduction of tree height with increasing elevation was site-specific and varied between 2 and 17 m per 100 m [31]. At elevations between 1700 and 1900 m in the Sellrain Valley (47° 13' N, 11° 06' E) in Tyrol, Austria, annual height growth of *Pinus cembra* L. decreased with increasing elevation by approximately 5 to 6% per 100 m, corresponding to the decrease in length of the growing season [19]. Paulsen et al. [31] found that annual radial increments of *Pinus cembra* linearly decreased with increasing elevation in the first part of the 19th century, and after 1940, average tree-ring width within the subalpine zone was similar, irrespective of the elevation. Rolland et al. [34] also reported that macroclimate change induced an increase in radial growth of four coniferous species (*Picea abies* (L.) Karst., *Larix decidua* Mill., *Pinus*

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cembra L. and *Pinus uncinata* Mill. ex Mirb.) growing in the French Alps near the upper treeline since 1750. Innes [13] related the worldwide increase in radial growth of subalpine trees to the macroclimate change since 1850. However, to our knowledge no studies have investigated the effects of microsite related to microclimate on tree growth within the subalpine zone. Indeed, tree life/growth is strongly controlled by the micro-environmental conditions at and near the ground surface (e.g. microclimate) at high altitudes [3]. On the other hand, elevation, slope angle and aspect have a strong influence on radiation, temperature, evaporation, wind speed and snow accumulation (e.g. [2, 3]), as well as on soil erosion and transport, local water balance, etc. In other words, elevation and steepness (depression is not studied, see [23]) seem to be a substitute for the complexity of local environmental elements on a given aspect. Hence, our microsites were a combination of elevation and steepness. Therefore, we examined tree growth responses to microsite, across a 200 m transect in the subalpine zone of the Austrian Alps (in the summer of 1997), to answer: (1) Whether increasing elevation similarly affects tree growth in height, diameter and biomass; (2) Whether different microsites affect tree growth significantly; and (3) Whether tree responses to microsite change with tree size (age)?

2. MATERIALS AND METHODS

2.1. Site location and description

The study forests were located in the Schmirn Valley (11° 30' E, 47° 07' N) in Tyrol, Austria, and extended from an elevation of 1900 to 2100 m on a south-facing slope. The uppermost native adult trees (larch, spruce) in this area are found at ca. 2000 m elevation. The original larch-spruce forest was heavily exploited between the 12th and 19th century [36]. Before the afforestation, the sites were used historically for grazing (H. Aulitzky, 1997, personal communication). The characteristic vegetation at the onset of the afforestation consisted of *Rhododendrum ferrugineum* L., *Vaccinieta* and *Calluneta*, etc. [36]. The soils, which had a thin humus layer (< 2 cm), belong to the podsollic brown type derived from siliceous slate. Stern [36] used the data (1902–1950) for Brenner (1370 m a.s.l.), located ca. 10 km south of the Schmirn Valley (1400 m a.s.l.), to determine the following climatic characteristics for the Schmirn Valley: annual mean temperature 4–5 °C; mean temperature in July 13.6 °C; mean temperature in January –4.9 °C; mean annual precipitation 1033 mm (of which 25–33% falls as snow). Given the approximate 500 to 700 m difference in elevation from the valley (1400 m) to the study sites (1900 to 2100 m), and a mean temperature gradient of 0.6 °C/100 m, temperatures on the sites are approximately 3 to 4 °C lower than those in the valley during the growing season.

2.2. Forest stands and plots

The study forests (24 ha) were planted by the Tyrolian Section of Torrent and Avalanche Control in 1972 with 5 years old seedlings (Seeds were collected at ~1900 m elevation in Innervillgraten (46° 40' N and 12° 25' E), East-Tyrol, Austria; J. Neuner, 2001, personal communication). According to the cluster afforestation technique (Rottenstruktur; [24, 35]), i.e. 3–4 seedlings per group (Rotte) were planted at a spacing of 2 × 2 m. The seedling survival was ~ 25% near the treeline and ~ 50% in the lower part. No thinning or addition of fertilizer was done on any of the plots in the past. However, if a tree was infected by *Herpotrichia juniperi* (Duby) Petr. or/and *Phacidium*

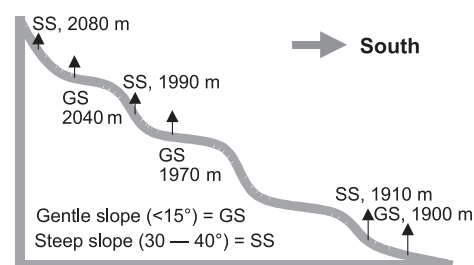


Figure 1. Location of plots. Three plots were chosen and studied for each elevation on a south-facing slope in the Schmirn Valley, Tyrol, Austria.

infestans Karst., it was removed and burned (J. Neuner, 2001, personal communication).

According to our given criteria, i.e. two slope angles (steepness; GS = gentle slope with < 15° vs. SS = steep slope with 30–40° slope angle) along altitudinal gradients on a south-facing slope, 18 plots were selected in this forest (Fig. 1). As described above, the combination of elevation and steepness is defined as microsite. The size of “microsite” ($r \leq 25$ m) is defined in this study after Blüthgen [6] and Barry [3]. The plot size (πr^2) was 100 m² ($r = 5.65$ m), depending also on the size of the selected microsites, since all study plots must always be within the forest at each microsite in order to avoid the edge effects on tree growth. Each plot consisted of 20 to 45 trees. The trees studied were 28 years old.

2.3. Tree measurements and data analysis

Height and diameter (breast-height diameter or diameter at the trunk base when trees were smaller than 1.3 m tall) of all healthy trees (individuals without clear signs of damage in the past) were measured in the summer of 1997 (measured data excluding growth in 1997). Three to five average size trees were chosen in each plot for the annual height increment and the cumulative height measurements. Two or three of these trees were cut for analysis of the annual radial growth (at trunk base in 0 cm stem height) and for estimation of needle, branch, stem and root biomass. The roots were excavated manually and the lost root fraction was estimated from the root diameter at the broken point in order to optimize below-ground biomass estimation. In other words, we utilized a root diameter/dry mass function (not shown) to reconstruct the terminal lost root mass of broken roots. All biomass components were weighed after oven-drying at 75 °C for 3 days at the University of Innsbruck. The ring width was measured (precision 0.01 mm) and recorded with a digital position meter in combination with a microscope (25×–40×) (Digitalpositionmeter Typ I, L. Kutschenreiter, Vienna) at the Vienna University of Agricultural Sciences. The average growth of tree-rings formed at the same cambial age was calculated and presented for each microsite. Stand biomass was estimated by mean tree density per hectare multiplied by mean mass per tree for each microsite.

Mean values of growth (cumulative height, annual height increment, tree-ring, biomass) for each plot were calculated. First, the data of the cumulative height were analyzed using two-way ANOVA to determine the effects of elevation, steepness and their interaction on cumulative height growth of trees (data not shown because no effects of interaction between elevation and steepness on tree growth were found, till to the age of 28 years). The data were therefore analyzed using a single factor ANOVA and Tukey’s test (Software JMP, SAS Institute) for the difference between the means of replicates as well as between the means at different microsites [9]. Using the height growth

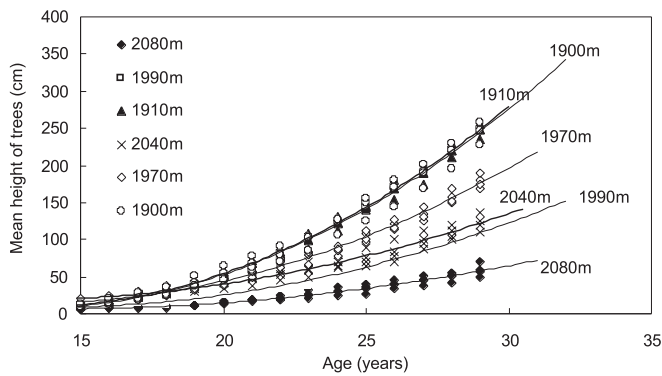


Figure 2. Cumulative height in relation to age of *Pinus cembra* trees growing at different microsites (1900, 1970 and 2040 m on GS, 1910, 1990 and 2080 m on SS) in the Schmirn Valley, Tyrol, Austria.

data measured from 11 to 28 years old of trees, a polynomial and an exponential model were used for the regression analysis of cumulative height growth and annual height increment in relation to age of trees at each microsite, respectively.

3. RESULTS

3.1. Cumulative and annual height growth

Cumulative height growth decreased with increasing elevation (Fig. 2). Steepness seems to have no influence on height growth at lower elevations (GS at 1900 m vs. SS at 1910 m; Fig. 2), whereas it led already to a statistically significant difference ($P = 0.026$) in mean cumulative height between 1970 m (GS) and 1990 m (SS) at the age of 16 years (data not shown). The difference in mean cumulative height among the plots at the six altitudes was significant ($P = 0.019$ at the age of 16 years) for trees ≥ 16 years old. However, among the plots on SS, the difference in tree height became statistically highly significant ($P < 0.001$), when trees reached the age of 19 years, whereas on GS, it took two more years (age 21) for the trend to become significant ($P = 0.003$). At the age of 28 years, the mean cumulative height of trees decreased with increasing elevation by 136 cm per 100 m on SS, and by 108 cm on GS (data not shown). Mean cumulative height (H) of trees in relation to tree age (y ; available for $17 \leq y \leq 55$) can be described by (Fig. 2):

(1) On SS: For plots at 1910 m a.s.l.: H (cm) = $0.9573y^2 - 25.155y + 173.2$; $R^2 = 0.99$; For plots at 1990 m a.s.l.: H (cm) = $0.5144y^2 - 15.179y + 121.85$; $R^2 = 0.98$; For plots at 2080 m a.s.l.: H (cm) = $0.211y^2 - 4.7301y + 21.672$; $R^2 = 0.96$;

(2) On GS: For plots at 1900 m a.s.l.: H (cm) = $0.9343y^2 - 24.286y + 164.86$; $R^2 = 0.99$; For plots at 1970 m a.s.l.: H (cm) = $0.7925y^2 - 23.198y + 189.08$; $R^2 = 0.99$; For plots at 2040 m a.s.l.: H (cm) = $0.4909y^2 - 14.404y + 130.19$; $R^2 = 0.96$.

Annual height increment (h) increased with increasing tree age (y) and it decreased with increasing elevation (Fig. 3). h decreased with increasing elevation by about 35% per 100 m on GS and 43% on SS at the age of 28 years (data not shown). The relationship between h and y (available for $11 \leq y \leq 55$) can be simulated by (Fig. 3):

(1) On SS: For plots at 1910 m a.s.l.: h (cm) = $0.7168e^{0.1314y}$; $R^2 = 0.91$; For plots at 1990 m a.s.l.: h (cm) = $0.6435e^{0.1067y}$;

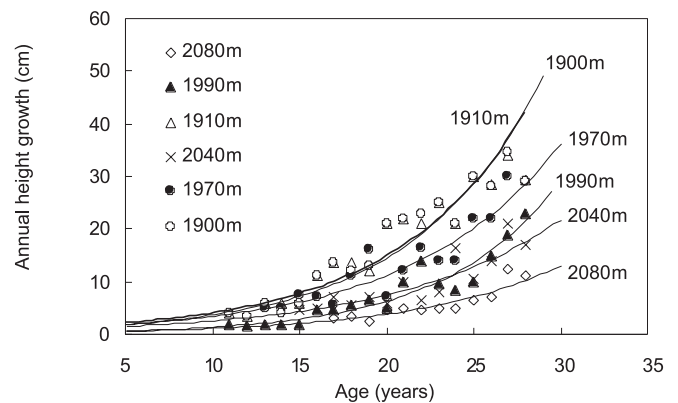


Figure 3. Annual height increment (mean values; $n = 3$) in relation to age of *Pinus cembra* trees growing at different microsites (1900, 1970 and 2040 m on GS, 1910, 1990 and 2080 m on SS) in the Schmirn Valley, Tyrol, Austria.

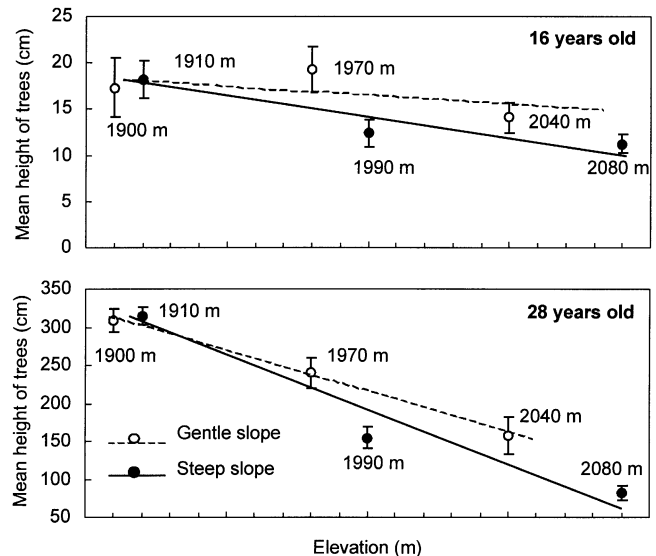


Figure 4. Mean height (\pm SE, $n = 3$) of trees (16 vs. 28 years old) growing at different microsites on a south-facing slope in the Schmirn Valley, Tyrol, Austria. At 16 years old, the lines, both on GS (gentle slope) and SS (steep slope), showed a small slope, which indicated the limited effects of elevation on height growth of trees. At 28 years old, the lines had more steep slope indicating the marked effects of elevation.

$R^2 = 0.81$; For plots at 2080 m a.s.l.: h (cm) = $0.1841e^{0.1537y}$; $R^2 = 0.92$;

(2) On GS: For plots at 1900 m a.s.l.: h (cm) = $0.74e^{0.1179y}$; $R^2 = 0.85$; For plots at 1970 m a.s.l.: h (cm) = $0.6268e^{0.1364y}$; $R^2 = 0.89$; For plots at 2040 m a.s.l.: h (cm) = $0.2327e^{0.122y}$; $R^2 = 0.85$.

Elevation and steepness (SS and GS) had no important influence on height growth of trees during the young age phase within 16 years (Figs. 2, 3 and 4). As trees got older (larger), elevation affected the height growth markedly, especially on SS (Fig. 4).

Table I. Dry biomass (mean values) and biomass fractions (% of total tree biomass) of *Pinus cembra* trees at different microsites on a south-facing slope in the Schmirn Valley, Tyrol/Austria⁽¹⁾.

Steepness	Steep slope			Gentle slope		
	2080 m	1990 m	1910 m	2040 m	1970 m	1900 m
Elevation						
Branches						
Biomass (g)	396 ^a	735 ^b	2 315 ^c	1 235 ^a	2 578 ^b	2 859 ^c
% of the total tree biomass	(31.6%)	(18.2%)	(23.7%)	(22.3%)	(25.5%)	(25.3%)
Needles						
Biomass (g)	401 ^a	961 ^b	2 536 ^c	1 634 ^a	2 470 ^b	2 788 ^c
% of total tree biomass	(32.1%)	(23.8%)	(26.0%)	(29.6%)	(24.5%)	(24.6%)
Stem						
Biomass (g)	228 ^a	1 030 ^b	3 054 ^c	1 164 ^a	2 758 ^b	3 607 ^c
% of total tree biomass	(18.1%)	(25.5%)	(31.3%)	(21.1%)	(27.3%)	(31.8%)
Roots ⁽²⁾						
Biomass (g)	226 ^a	1 315 ^b	1 852 ^c	1 496 ^a	2 290 ^b	2 073 ^c
% of total tree biomass	(18.2%)	(32.5%)	(19.0%)	(27.0%)	(22.7%)	(18.3%)
Below-/above-ground biomass	0.22	0.48	0.23	0.37	0.29	0.22
Total tree biomass (g)	1 251 ^a	4 041 ^b	9 757 ^c	5 529 ^a	10 096 ^b	11 327 ^c
Tree density (trees·ha ⁻¹)	2 400	2 800	4 100	4 200	3 700	4 000
Total stand biomass (t·ha ⁻¹)	3.002	11.315	40.004	23.222	37.355	45.308
Mean growth per tree (g·year ⁻¹)	45 ^a	144 ^b	348 ^c	197 ^a	361 ^b	405 ^b
Mean biomass accumulation (kg·ha ⁻¹ ·year ⁻¹)	107	404	1 429	829	1 334	1 618

(1) Different letters indicate statistically significant ($p < 0.05$; $n = 3$) difference within a group of steepness (steep slope or gentle slope).

(2) Including root system.

3.2. Diameter growth

In contrast to tree height growth, no clear relationship between radial growth and microsite was found (Fig. 5). For example, tree-rings at 2040 m on GS were similar with those at 1910 m on SS and wider than those at 1970 on GS and 1990 m on SS (Fig. 5). However, this effect may result partially from the difference of tree densities between stands at different microsites (Tab. I), for example, tree density at 2040 m (GS, 4200 trees·ha⁻¹) was higher than that at 1990 m (SS, 2800 trees·ha⁻¹). Higher tree density can lead to create a forest microclimate some early, and thereby positively influenced radial growth.

3.3. Biomass

Total tree biomass decreased drastically with increasing elevation both on GS and SS (Tab. I). On SS, total tree biomass at 2080 m was only 13% (1251 g) of that at 1910 m (9757 g), whereas the annual mean growth rate declined from 348 g·year⁻¹ to 45 g·year⁻¹ (-87%), the corresponding annual biomass growth declined with increasing elevation by 178 g per 100 m. Similarly, the total tree biomass at 2040 m was only 49% (5529 g) as compared to 1900 m (11 327 g) on GS, correspondingly, the annual mean growth rate declined from 405 g·year⁻¹ to 191 g·year⁻¹ (-51%), and annual biomass growth declined with increasing elevation by 153 g per 100 m (Tab. I). Total stand biomass and mean biomass accumulation per year decreased also with increasing elevation, which depend on both total tree biomass and tree density (Tab. I).

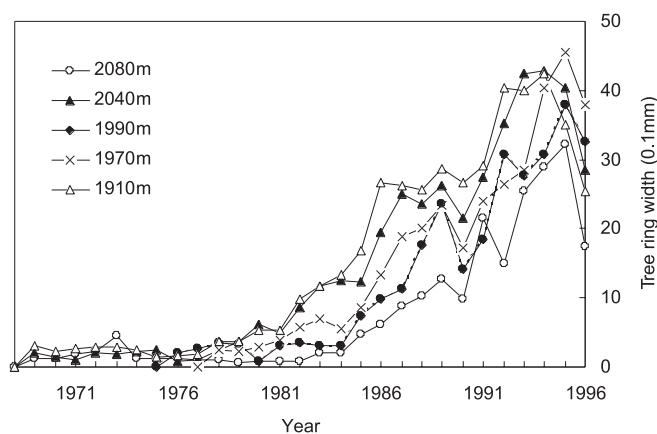


Figure 5. Mean radial growth ($n = 3$) at the base (0 cm stem height) in relation to age at different microsites (1970 and 2040 m on GS; 1910, 1990 and 2080 m on SS) on a south-facing slope in the Schmirn Valley, Tyrol, Austria. For the sake of clearness, we omitted data of trees at 1900 m (GS), because they are very similar with those of trees at 1910 m.

The fraction of needles increased with increasing elevation both on GS and SS, whereas the stem fraction showed a decreasing trend, and the branch and root fraction did not show any clear trend (Tab. I and Fig. 6).

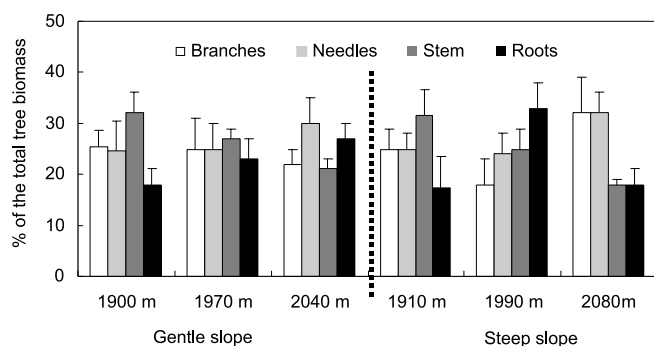


Figure 6. Biomass fractions (%; mean values + SE; $n = 3$) of total tree biomass at different microsites on a south-facing slope in the Schmirn Valley, Tyrol, Austria.

4. DISCUSSION

4.1. Height growth reduction with increasing elevation

The reduction of height growth with increasing elevation confirmed earlier observations made for *Picea abies* [12, 22, 30, 37] and *Larix decidua* [22, 30, 37], as well as for *Pinus cembra* [5, 15, 16, 18, 19, 28, 31, 37]. However, the reduction rate differs among various studies (e.g. for *Pinus cembra*, [19, 31]). For instance, spruce height growth in the Seetal Alps, Austria, proceeded at a mean annual growth of 33 cm in the valley at 700 m but only 8 cm in the zone above the timberline at 1900 m [12]. The annual height growth of spruce seedlings at 1900 m was found to reach only 20% of the maximum value at the optimum altitude of 1250 m in the Wipptal in Austria [37]. However, Ott [30] reported that no change in the height of mature trees with a dbh larger than 30 cm was detectable for larch and spruce (at elevations well below the treeline up to 1800 m on a south-facing slope and up to 1900 m on a north-facing slope in the Lötschertal, Switzerland).

Since the annual height increment increased with increasing age and decreased with increasing elevation, the difference in cumulative height of trees growing at different elevations increased and became significant with time. When trees were very young, their annual height increment and cumulative height growth did not differ with an increase in elevation. This study revealed that elevation began to significantly affect the growth of trees growing within the subalpine zone only when trees reached a certain age or exceeded a certain size (0.5 m; [23]).

4.2. Diameter growth

Normally, tree density has a marked effect on diameter growth [17]. However, we did not find a clear relationship between tree-ring width and different tree densities at different elevations both on GS and SS since the trees/stands studied did not fully cover the ground surface. The small diameter growth of trees in the early life stage possibly resulted from the severe competition of grasses [1, 33] and from the snow cover [22]. We did not find a significant relationship between elevation and

radial growth. As various site factors influence diameter growth, its correlation with elevation is less pronounced than height growth [37]. This phenomenon has been highlighted for *Nothofagus solandri* [27, 40], for *Pinus cembra* [31], and for *Picea abies* and *Larix decidua* [23] in subalpine areas as well. Also, Däniker [7] and Oswald [29] have shown that diameter increment declined less with increasing elevation than height growth. The study by Weber [42] also showed no difference in mean radial growth of *Larix decidua* (100–400 years old) growing between 1700 and 2200 m a.s.l. in the Upper Engadine Valley, Switzerland. However, Tranquillini [37] found that the annual radial increment of spruce in the Seetal Alps, Austria, was 6 mm at low and moderate elevations (< 1600 m), falling rapidly to 3 mm at timberline (1900 m). Similarly, Mork [26] measured a decline in diameter increment for spruce from 5.0 mm at 140 m to 1.5 mm at 860 m elevation in southern Norway. Kienast [14] found that the annual radial growth of subalpine trees depended on the precipitation in winter and in early spring. A recent study by Meyer [25] revealed that the ring width of trees (*Picea abies*, *Pinus cembra*) growing near the alpine timberline in Switzerland was positively correlated to the summer temperature (June, July) [20] and did not vary with a change in elevation (140 m difference). In contrast, Norton [27] did not find a statistically significant effect of summer temperature or annual precipitation on the tree-ring width of *Nothofagus solandri* along an elevational gradient from the valley floor (800 m) to alpine timberline (1400 m) in New Zealand.

4.3. Biomass

Tree biomass showed a clear reduction with increasing elevation. In Austria, Benecke [4] found that seedling dry mass production at 1950 m (timberline) compared with that at 650 m (valley) reduced by 42% in *Pinus mugo*, 54% in *Picea abies*, and 73% in *Nothofagus solandri* var. *cliffortioides*. In the Craigieburn Range, New Zealand, Wardle [41] found in seedling establishment trials that dry matter production of *Nothofagus solandri* decreased by 60% from 1100 to 1600 m altitude.

The effects of elevation and steepness on height, biomass and diameter growth were highly, less and not significant, respectively (question 1 of the Introduction). This difference may have resulted from more stunted morphology as well as the higher density of tree tissues in the uppermost area near the treeline. Perterer and Körner [32] found that the dry matter of 100 needles of *Picea abies* trees growing near the treeline at 1900 m was significantly heavier than that at mid-elevation between 500 and 1500 m, and the latter was not statistically different from the lowland value (< 500 m) near Innsbruck, Tyrol, Austria. Hence, (1) *Pinus cembra* at the highest altitude had similar biomass increment compared with that at 200 m lower within a subalpine zone [28], and (2) a study from Bernoulli and Körner [5] showed no elevational trend in total tree biomass in a similar afforestation (25 years old) in *Pinus cembra*, *P. uncinata* and *Larix decidua* between 2080 and 2230 m elevation on a northeast slope in Stillberg/Davos, Swiss Alps.

In the subalpine zone, the forest stand opens up and trees are isolated from each other. Hence, trees are influenced more and more by elevation associated with local environmental conditions, and once above the treeline, woody plants are not able (to grow) to reach a tree height (3 m; according to [31]) and are

krummholz [37]. However, the elevation effects on tree growth also depend on tree size/age (question 3 of the Introduction). Hence, the effect of elevation on growth of subalpine trees seems to be size-specific [23]. The effects begin to occur when trees reach a certain size. For example, the entire annual height increment can be destroyed by frost damage (water deficit) in late winter [37, 38] or other damages (e.g. [11]), such as when trees attain ca. 0.5 m in height above the snow surface where the risk of weather damage was assumed to be at its maximum [21, 37].

4.4. Micro-environmental conditions associated with microsite

Macroclimate is modified by topography and vegetation to local climate (mesoclimate), the latter is modified again to microclimate by microsite. Microsite can also lead to an edaphic, hydrological and vegetational differentiation within a small space, especially in the subalpine areas. Microrelief of 50 m ($r = 25$ m) or less can affect the distribution of precipitation [3] and can also change the distribution and duration of snow cover [2], which can strongly affect the soil climate (e.g. root zone temperature), erosion, moisture and nutrient supply [16, 23]. Radiation and temperature depend on slope angle and aspect, which can affect the local water balance. For example, Turner [39] measured extreme temperature of 80 °C on dark humus at 2070 m elevation on a southwest aspect with 35° slope in the Ötztal, Austria, during July 1957. In subalpine areas of the Northern Hemisphere, strong radiation and high temperature, together with strong wind and high evaporation on steep south-facing slope can lead to a limit of available soil moisture during the growing season, which may negatively affect tree growth in the alpine treeline ecotone. Deep snow layers present in late winter can encourage *Herpotrichia juniperi* (Duby) Petr. and *Phacidium infestans* Karst., which usually damage or destroy the subalpine trees on gentle slope [8, 10]. Therefore, microsite related to micro-environmental conditions can control growth rate of subalpine trees (question 2 of the Introduction).

5. CONCLUSION

We suggest that elevational effects gradually become the determinate factor of tree growth as trees get taller in subalpine areas. In the seedling stage, neither steepness nor elevation has a strong effect on growth. Once the seedlings exceed a certain height (> 0.5 m), elevation and steepness have a significant influence on growth. But, elevation affects tree growth significantly, irrespective of steepness, as tree canopies fully cover the ground surface and create a forest microclimate. Over the range of subalpine elevations studied here, we conclude that microclimate associated with microsite controls growth during the early life stages of trees. Once trees/stands create a forest microclimate, topography related to local climate determines growth. In other words, the microsite conditions may determine whether a seedling can grow (and reach) a tree height of 3 m (thereby create a forest microclimate). Hence, finding and choosing suitable microsites with suitable micro-environmental conditions are very important for a successful restoration of forests in so-called “kampfzone”.

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