



1 Radial growth of *Picea abies* is controlled by joint effects of 2 temperature and nutrient availability at the lower part of treeline 3 ecotone

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8 **Abstract.** Treeline ecotones in complex mountain landscapes are exposed to pronounced differences in irradiation and soil
9 nutrient availability. Different amounts of nutrients and direct solar energy can influence tree stem growth resulting in
10 variation of growth rates and growth phenology across lower parts of treeline ecotone. We hypothesized that at two
11 contrasting sites located on north and south-facing slopes, differences in nutrient availability outperform temperature
12 differences in modulating stem growth rates while growth phenology is driven by the course of seasonal temperature. To test
13 this hypothesis, we compared the growth phenology and kinetics of *Picea abies* in the lower part of treeline ecotone between
14 a north-facing slope with relatively nutrient-rich soils and a south-facing slope with nutrient-poor soils. We analysed intra-
15 annual wood formation and its response to ambient climate, as well as soil and air microclimate and soil and needle nutrient
16 content. Our results showed that thermal differences in treeline ecotones between south and north-facing slopes in temperate
17 mountains are small but nontrivial involving higher daytime temperatures at south-facing slopes and longer irradiation of
18 north-facing slopes during the middle part of growing season. The timing of growth onset and maximum growth rate were
19 almost identical on both slopes. Accordingly, annual stem growth at both sites was most sensitive to the meteorological
20 conditions at the start of the growing season and around the summer solstice. However, the absolute growth rate was higher
21 on the north-facing slope, consistent with a higher availability and content of base cations in the soil and the needles. Our
22 results suggest that temperature governs growth phenology at the lower part of the treeline ecotone, but nutrient availability
23 modulates the growth rate in the peak season when temperature no longer limits cambial activity. We conclude that the effect
24 of nutrient availability can be superior to the effect of slope aspect for stem growth rates of *Picea abies* located in the lower
25 part of treeline ecotone in temperate mountain range.

26 1 Introduction

27 In cold environments, tree stem growth is tightly linked to temperature oscillations during the growing season (Rossi et al.,
28 2016; Körner, 2021), which is reflected in the seasonal phenology of wood formation, that is, cambial division and xylem
29 differentiation (Cuny et al., 2015). There are minimum temperature thresholds for both photosynthesis and the processes



30 linked to the investment of non-structural carbohydrates into developing xylem, the latter being lower and thus representing
31 the ultimate limitation of stem growth (Fatichi et al., 2019). This is apparent along elevation transects where both non-
32 structural carbohydrates and nutrient contents in twigs, leaves and sapwood increase towards the treeline as a result of
33 increasing sink limitation of the growth (Hoch and Körner, 2012; Fajardo and Piper 2017; Doležal et al., 2019). While no
34 exceptions from pure sink limitation of tree growth have been found for broadleaf treelines in the southern hemisphere
35 (Fajardo and Piper 2017), some studies examining conifers in permafrost zone have highlighted the important role of nutrient
36 availability in co-limiting stem growth (Sullivan et al., 2015; Dial et al., 2022). Although this is probably not generally valid
37 for conifer treelines outside the permafrost zone (Hagedorn et al. 2020; Körner, 2021), the nutrient and moisture co-
38 limitation of tree growth can play a role at local upper tree limits (boundaries of realized niche) or in the lower part of
39 treeline ecotone, several tens to hundred meters below treeline (Möhl et al., 2018, Körner and Hoch, 2023).

40 The low-temperature limit of tree growth at its cold range boundary is evidenced by growth resumption after exceeding a
41 certain temperature threshold, as shown both by warming/cooling experiments (Gričar et al., 2006; Lenz et al.; 2013) and by
42 observations in natural treeline settings (Körner and Hoch, 2006; Rossi et al., 2007). Indirectly, the prevailing low-
43 temperature limitation of tree growth at cold sites is supported by similar thermal limits of global treelines, i.e., cold margins
44 of the tree life form distribution (Körner and Paulsen, 2004). Furthermore, tree-ring chronologies from treelines are
45 significantly correlated with growing season temperature (Chagnon et al., 2023), and calibrated thermal limits of wood
46 formation models agree with those based on direct or experimental observations (Tumajer et al., 2021).

47 Recently, tree growth in cold biomes tends to accelerate in some areas, which has often been attributed to warming and an
48 extension of the growing season (Shi et al., 2020). However, in forest stands near treeline, observed growth enhancement has
49 been connected to increased nitrogen supply in some regions (Kolář et al., 2015; Möhl et al., 2018; Etzold et al., 2020).
50 Sullivan et al. (2015) showed better performance in shoot, stem and root growth at microsites relatively richer in nitrogen at
51 the Arctic treeline due to warmer soils and a higher snowpack accelerating nutrient cycles (Dawes et al., 2017). Not only
52 nitrogen (N) but also phosphorus (P, and namely the stoichiometry of N and P) was suggested as a limiting factor of tree
53 occurrence at some treeline ecotone sites in the Himalayas (Müller et al., 2017). Apart from N and P, the role of other
54 nutrients, especially base cations, has been largely neglected at tree stands near their cold distribution margins. Recently,
55 there is a growing body of literature showing that base cations can play a vital role under certain conditions in limiting tree
56 growth in the treeline ecotone (Drollinger et al., 2017) or in montane forests (Körner, 2022; Oulehle et al., 2023).

57 Local evidences of growth enhancements at sites relatively enriched by N and P are not necessarily in conflict with the
58 ultimate role of low temperature limitation of tree growth at treeline (Körner, 2012) and with observations of increasing
59 nutrient concentrations in leaves with elevation near cold margins of tree distribution (Fajardo and Piper, 2017). They rather
60 suggest that nutrient availability together with low temperature might co-determine growth dynamics at upper tree limits
61 whose position lags behind the pace of warming (Fatichi et al., 2019). As many current upper tree limits cannot follow the
62 upward shift of isotherms (Körner and Hiltbrunner, 2024), the understanding the importance of climate, nutrient availability,



63 and their interaction as determinants of the growth dynamics becomes critical in a period of unprecedented impacts of
64 warming on mountain ecosystems.

65 In a complex mountain relief, a high variation in topoclimate and soil conditions can create a heterogenous mosaic of sites
66 differing in local surface temperature (Körner, 2012; Jochner et al., 2017; Kuželová et al., 2021) as well as nutrient content
67 (Liptzin et al., 2013, Mayor et al., 2017). Probably the best-known topoclimatic effect is the so-called slope exposure
68 phenomenon, which suggests that south-facing slopes in the northern hemisphere outside the tropics are warmer than north-
69 facing slopes, and vice versa in the southern hemisphere (Körner, 2012). This phenomenon is less pronounced on forested
70 slopes (Paulsen et al., 2001). Sites on opposite slopes might differ not only in insolation and surface temperature but also in
71 nutrient availability, as surface temperature might influence litter decomposition through surface moisture and snow melt
72 patterns (Dawes et al., 2017; Ellison et al., 2019; Stark et al., 2023).

73 Therefore, an experimental design employing opposite south-facing (S-slope) and north-facing slopes (N-slope) at the same
74 elevation provides an excellent natural settings where organisms are exposed to pronounced differences in incoming solar
75 radiation under a similar macroclimate. Such a design has previously been used to test various ecological hypotheses related
76 to tree growth and its limiting factors (Rossi et al., 2007; Moser et al., 2010; Tyagi et al., 2023). In this study, we use an
77 opposite slope aspect design in a complex research setting, which allows us to cover multiple site properties that potentially
78 influence tree growth performance in the lower part of the treeline ecotone. We carried out detailed observations of *Picea*
79 *abies* trees in terms of intra-annual wood formation and inter-annual climate-growth responses of radial stem growth together
80 with analyses of site thermal and moisture properties and soil and foliar nutrient content. We agree with and test the general
81 assumption that at the lower part of treeline ecotone, the crucial phases of tree growth, such as growth resumption and timing
82 of the peak growth rate, are driven by thermal and solar constraints (Rossi et al., 2006b; Rossi et al., 2007). However, we
83 hypothesize that the absolute growth rate in the middle part of the growing season is influenced by nutrient availability,
84 given the positive effect of nutrient availability on absolute tree growth that has been shown at some cold-limited sites (Möhl
85 et al., 2018; Sullivan et al., 2015).

86 **2 Material and Methods**

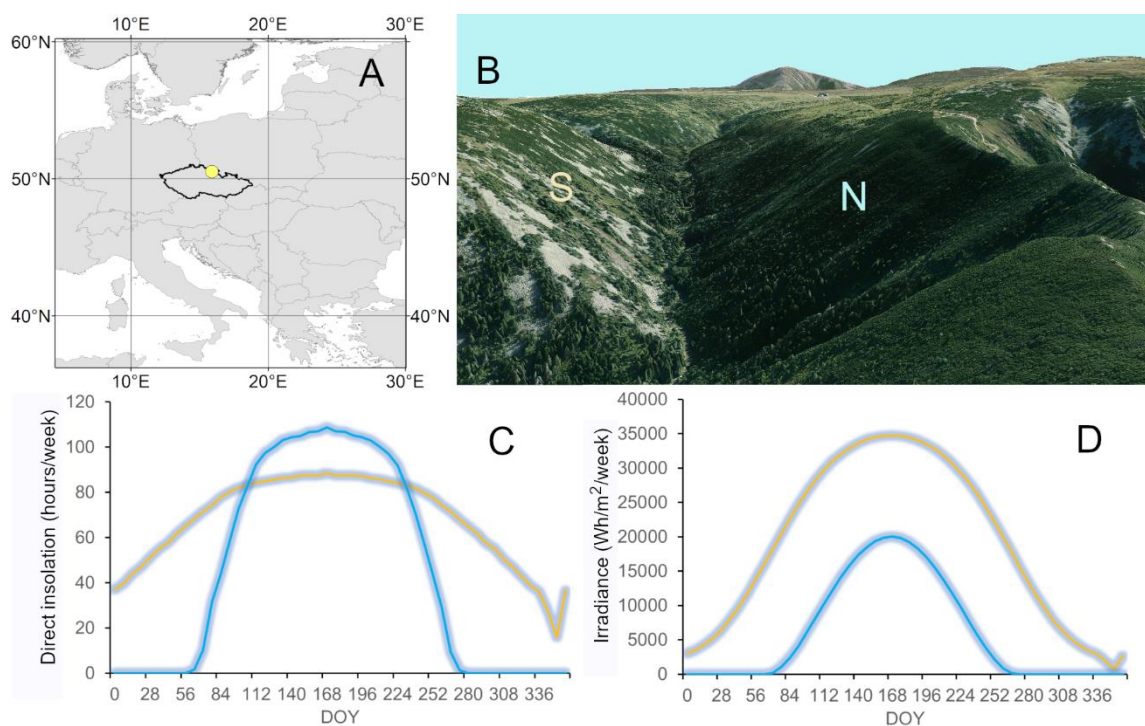
87 **2.1 Study area**

88 Our study focuses on *Picea abies* [L.] Karst. growing on N and S-slopes in the treeline ecotone in the Krkonoše Mts, Czech
89 Republic (50°43'N, 15°40'E, site elevation 1250 m a.s.l., Figure 1). The Krkonoše Mts, with the highest peak Mt Sněžka
90 (1602 m a.s.l.), are characterized by high annual precipitation sums (on average 1400–1600 mm) and a mean annual
91 temperature of 0.5°C in the uppermost locations (Metelka et al., 2007). Snow cover in the treeline ecotone lasts from
92 November until May, with a maximum snow depth of about 2 m (Metelka et al., 2007). The treeline ecotone is situated at
93 elevations ranging from 1250 to 1450 m.



94 Two sites on opposite slopes (N-slope, S-slope) were established in the lower part of the treeline ecotone in the Bilé Labe
95 valley (Figure 1). The canopy cover at both sites was 20 %, and the tree height of adult individuals ranged between 8 and 13
96 m. Both sites are located on steep slopes (inclination between 20° and 30°) with frequent patches of screes. The N-slope site
97 is located on the transition between gneiss and mica-schist (upper part) and granodiorites (lower part). The S-slope site is
98 underlain by granites. Skeletic Leptosols and Skeletic Podzols are the dominant soil types on the S-slope, and the same soil
99 types prevail on the N-slope, with patches of Histic Skeletic Podzols.

100



101

102 **Figure 1: (A) Location of the study area in Europe; (B) View from the west on the study sites (modelled by ArcScene; ESRI, 2020).**
103 **Modelled duration of direct insolation (C) and irradiance (D) plotted against the day of year (DOY) on the north-facing (N, blue)**
104 **and south-facing (S, orange) sites.**

105 2.2 Microclimatic monitoring

106 We measured air and soil temperature and soil water potential to characterize site micro-climatic conditions from 2012 to
107 2015 (to 2014 for soil water potential). Air temperature was recorded using sensors in radiation shields hanging in the tree
108 crown approximately 7 m above the ground (one sensor at each site). Three sensors recorded the soil temperature and soil
109 water potential of the root zone (mineral soil, -10 cm depth) per site at microsites fully shaded by tree crowns. We used
110 gypsum block soil water potential sensors to measure available soil moisture (measuring range 0 to -2 MPa, Delmhorst, EMS
111 Brno). Air and soil temperatures and soil water potential were measured and stored at 1-hour intervals. Both air and soil
112 temperature sensors have an accuracy of $\pm 0.2^{\circ}\text{C}$ (www.emsbrno.cz).



113 For each year and site, we calculated various variables that characterize the intra-annual meteorological patterns that are
114 important for woody plants. Following Körner and Hiltbrunner (2018), we used soil temperature to define the duration of the
115 meteorological growing season, i.e., the period when meteorological conditions potentially permit wood formation. We used
116 the continuous period where soil temperature values were above 3.2°C, roughly corresponding to a mean weekly air
117 temperature of 0°C (Körner and Paulsen, 2004). For both sites and for all years, we identified dates of the start, the end, and
118 the duration of the meteorological growing season. Additionally, we computed mean air and soil temperature for the period
119 June to September per site and year. Lastly, we calculated degree days by integrating mean daily air temperatures exceeding
120 5°C for each site and year.

121 Site insolation was estimated using the ArcGIS Solar radiation tool (ESRI, 2020). Based on a digital elevation model with 5
122 m resolution, we modelled the duration of direct insolation in hours and the solar irradiance (W/m²) for both sites and each
123 day of the year. For each site, the insolation depended on the sun's position, slope aspect and inclination, and the location of
124 surrounding ridges and peaks that shaded the sites for certain parts of the day and year.

125 **2.3 Soil and foliar nutrient analyses**

126 Soil samples were collected in two campaigns in October 2013 and October 2023. In the first campaign, we took two soil
127 samples, and in the second campaign, we took three soil samples from the topmost 10 cm of the mineral soil at each site.
128 Each sample from each campaign was pooled from five subsamples distributed randomly over each study site and properly
129 mixed. Air-dried soils were sieved to remove the size fraction > 2 mm. Samples were analysed for exchangeable pH
130 (CaCl₂), cation exchange capacity (CEC), total soil N, soil organic carbon (C_{ox}), and plant-available concentrations of Ca,
131 Mg, K and P with Mehlich III extraction solution (Mehlich, 1984). Soil samples were analysed in the accredited laboratory
132 of the Research Institute for Soil and Water Conservation, Prague. Differences between sites in measured soil variables were
133 tested using the Kruskal-Wallis test implemented in R (R Development Core Team, 2023). For this purpose, we merged
134 samples from both campaigns.

135 To compare the nutrient concentrations in needles between sites and to validate whether they reflect nutrient availability in
136 soils, we collected current-year and previous-year needles from six trees at each site in October 2023. The long lag between
137 the sampling of wood formation (2012-2014) and the sampling of foliar macroelements (2023) might influence absolute
138 values of the determined elements because of their interannual variability, but not the difference between sites, which
139 remains constant (Novotný et al., 2018). Branches from the upper part of the crown were cut using a telescopic long-reach
140 pruner. Current- and previous-year needles were sampled from all cut branches and pooled per site. Pooled samples of 1000
141 current-year and 1000 previous-year needles were dried and then analysed for the content of main macro- and
142 microelements. The analyses of the main macro- and microelements followed a standard ICP Forests protocol (Rautio et al.,
143 2020). The foliage K, Ca, Mg and P was determined using ICP-OES after needle decomposition in a microwave oven. The
144 total S and N content was analysed using the Leco CNS element analyser (Elementar Analysensysteme GmbH, Germany).

145



146 **2.4 Wood formation**

147 Six (2012) to eight trees (2013-2014) at each site were monitored in terms of wood formation (“xylogenesis”) over the three
148 growing seasons (Table S1), which overlapped with the period of microclimatic measurements. A new set of healthy and
149 dominant/co-dominant trees was selected for sampling each season to avoid possible impacts of previous year’s sampling on
150 ongoing cambial activity, e.g., by the formation of traumatic resin ducts. Wood microcores were sampled using a Trephor
151 puncher (Rossi et al., 2006a) at a stem height of 1 ± 0.2 m. Each sample contained the xylem of the current year, the cambial
152 zone, the phloem, and one or more previous complete annual rings. The distance between adjacent sampling points on a stem
153 was always greater than 3 cm to avoid effects of sampling on wood formation. Sampling intervals ranged from 7 to 10 days
154 during the period from April to October, which significantly exceeds the typical duration of a growing season in a treeline
155 environment (Tremml et al., 2015). Once sampled, the microcores were immersed in a formaldehyde-ethanol-acetic acid
156 fixative. The laboratory procedures followed Gričar et al. (2006). The microcores were dehydrated using a successive series
157 of ethanol and xylol-substitute and were then embedded in paraffin. 12- μ m-thick cross sections were cut using a rotary
158 microtome. The paraffin was removed, and samples were dehydrated using a successive series of xylol-substitute and
159 ethanol solutions with descending/ascending ethanol concentrations. The cross sections were then stained with safranin and
160 astra blue and mounted on permanent slides using Canada balsam.

161 The cells in the following wood phenological phases were counted for each cross section under 400–500x magnification
162 using an optical microscope following Rossi et al. (2003): cells in the cambial zone, enlarging cells, wall-thickening cells,
163 and mature cells. The number of cells in each developmental stage was counted in three radial files and subsequently
164 averaged. The number of cells in the preceding tree ring was counted for three radial files and averaged. For each tree, the
165 start and end date of each developmental phase (onset of cambial activity, enlarging phase, cell wall thickening phase,
166 mature phase), and the overall duration of cambial activity were determined according to Rossi et al. (2007).

167 The counts of cells developed over the course of the growing season were fitted by a Gompertz function using the R package
168 CAVIAR (Rathgeber et al., 2018). Next, the following parameters were determined from the Gompertz equation for each
169 tree: the maximum daily cell production rate, the day of maximum cell production rate (both called critical dates, Rathgeber
170 et al., 2018), and the mean daily production rate in the period when 90 % of cells were formed. Between-site differences of
171 critical dates and production rates were tested using the Kruskal-Wallis test implemented in R (R Development Core Team,
172 2023).

173 Logistic regressions were calculated to identify temperature thresholds at which the wood formation resumes (Rossi et al.,
174 2008), with active/inactive wood formation as the explained binary variable and the 7-day backward mean soil and air
175 temperature as explanatory variables. Only observations before the summer solstice were considered (Tremml et al., 2019).
176 The start of the active wood formation was alternatively defined by the occurrence of the first new cells in the cambial zone
177 or the first enlarging cells. All calculations were performed in R (R Development Core Team, 2023).

178



179 **2.5 Climate-growth relationships of tree-ring chronologies**

180 Wooden cores were extracted at 1 m stem height from 30 randomly selected dominant and co-dominant individuals of *Picea*
181 *abies* at each site in October 2013 using an increment borer (5 mm in diameter). Following standard laboratory procedures
182 (fixation of cores to wooden supports, air-drying, sanding), tree-ring widths were measured using the WinDendro system
183 (scanner and software with semi-automatic ring detection) (Regent Instruments, 2021). The resulting tree-ring series were
184 visually and statistically cross-dated using PAST 5 software (Knibbe, 2013; Speer, 2010). We focused on high-frequency
185 (interannual) growth variability preserved in tree-ring data. Therefore, tree-ring series were standardized with a cubic
186 smoothing spline with a 40-year window length at a 50% frequency cutoff, and the autocorrelation was removed using
187 autoregressive modelling (Cook and Peters, 1981). The tree-ring chronology for each site was built by averaging tree-ring
188 series of individual trees. We calculated Pearson correlations between tree-ring chronologies and climatic time series with
189 daily resolution and run the correlation analysis for time spans from ten to thirty consecutive days (Jevšenak, 2019). Daily
190 climatic data (mean daily temperature, daily precipitation totals) from the nearest meteorological station Labská/Vrbatova
191 bouda (1320 m a.s.l., 8 km westwards from our sites) were available and used from 1961 after filling data gaps using the
192 neighboring station. Before calculating correlations, temperature data were standardized in the same way as tree-ring data
193 (Ols et al., 2023). Tree-ring and temperature data standardization and climate-growth correlations were performed using the
194 `dplR` (Bunn et al., 2023) and `dendroTools` (Jevšenak and Levanič, 2018) R packages (R Development Core Team, 2023).

195 **3 Results**

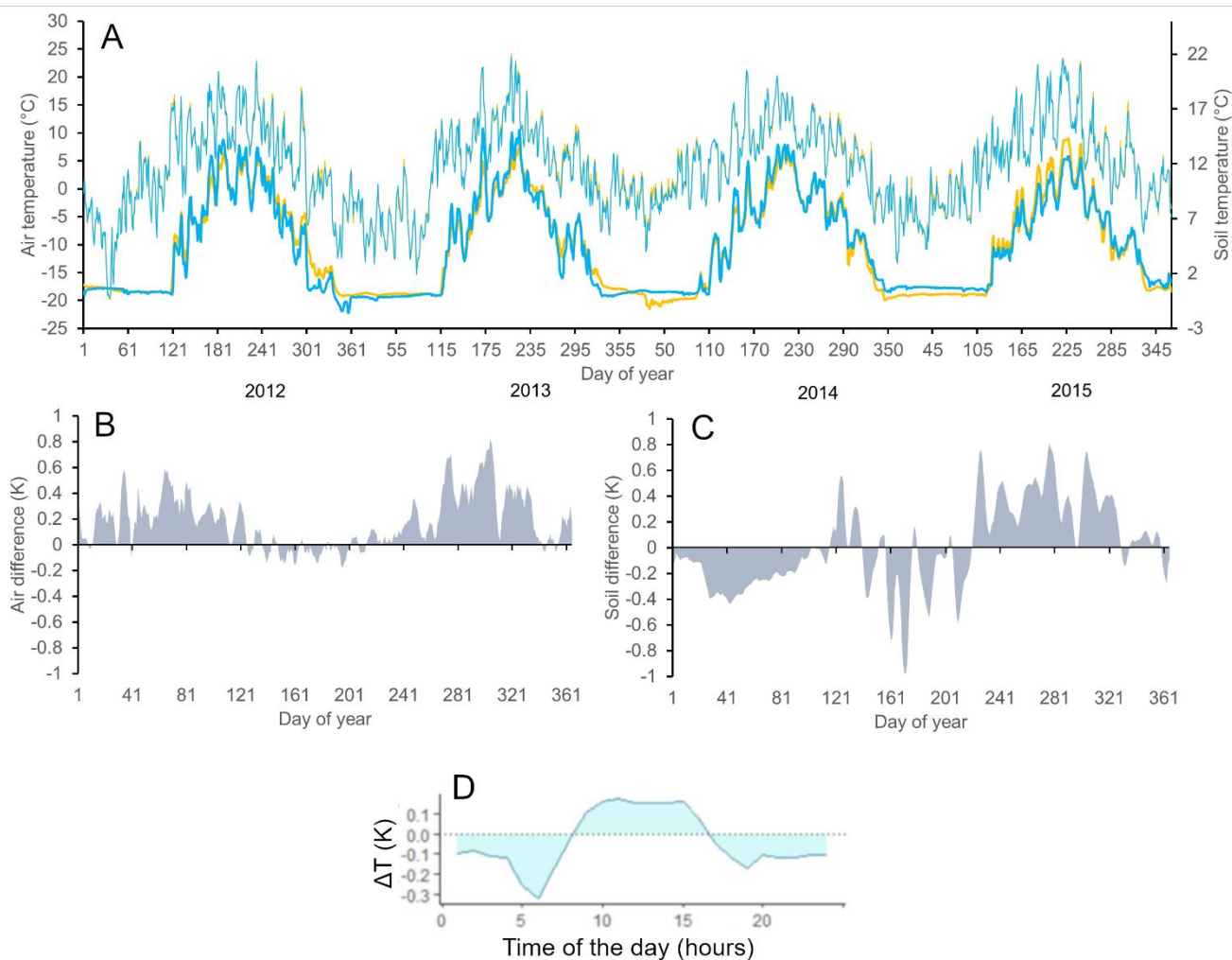
196 **3.1 Solar radiation and temperature differences**

197 Irradiance was considerably higher on the S-slope than on the N-slope over the entire year (Fig. 1D). The N-slope was
198 characterized by more than five months in winter without direct insolation (Fig. 1C). The duration of direct insolation was
199 accordingly longer on the S-slope except for the period between end of April and mid August when the weekly duration of
200 insolation was longer on the N-slope, reflecting the effect of the complex topographical setting (Fig. 1B, 2A, 2B). Mean air
201 temperature during the main growing season (June-September) was about 0.1 K higher at the S-slope in most years, but this
202 difference was smaller than the measurement error (Table 1). Similarly, degree days were slightly higher at the S-slope
203 (Table 1). Interestingly, differences in air temperature during the main part of the growing season showed a pronounced
204 daily pattern with a warmer S-slope during the day and a warmer N-slope at night (Fig. 2D).

205 At both sites, soil temperature oscillated under the snowpack close to 0°C usually until the day of year (DOY) 110-120 (ca.
206 end of April) and then abruptly increased (Fig. 2A). Soils tended to be cooler on the S-slope during the winter, possibly due
207 to deeper freezing under a thinner snowpack. Soil temperature was higher on the S-slope at the very beginning and towards
208 the end of the growing season, while soils on the N-slope tended to be warmer in the peak growing season (Fig. 2C), which
209 roughly corresponds to the period when daily direct insolation is longer on the N-slope (Fig. 1C). As a result, mean soil



210 temperature was slightly warmer (0.2-0.3 K) at the N-slope over the June-September period in most years, with differences
211 again being close to the measurement error, except in 2015 when the S-slope was substantially warmer (Table 1). There was
212 no systematic pattern in the duration of the meteorologically-defined growing season length (Table 1).
213 Both sites exhibited several periods with significant negative soil water potentials (Fig. S1), occurring mostly in the summers
214 of 2013 (both N- and S-slope) and 2014 (N-slope) but also in the winters of 2012 (N-slope) and 2014 (S-slope).



215
216 **Figure 2: (A) Daily means of soil (bold lines, bottom) and air temperature (thin lines, top) for the north- (blue) and south- (orange)**
217 **facing slope for the period 2012-2015. (B) Differences between south- and north-facing slopes (temperature south minus**
218 **temperature north) smoothed by a 5-day moving average 2012 – 2015 for mean daily air temperature and (C) the same for mean**
219 **daily soil temperature. (D) Differences in the course of daily air temperature (temperature south – temperature north; hourly**
220 **interval) for June-August 2012-2015.**

221
222



223 **Table 1: Thermal characteristics of the growing season on the north (N-slope) and south-facing (S-slope) site calculated based on**
 224 **on-site measurements.**

Year	Site	Growing season duration (days)	Mean Air T in June – September (°C)	Mean Soil T in June – September (°C)	Degree days exceeding 5 °C
2012	N-slope	145	11.26	9.96	1023
	S-slope	167	11.34	9.81	1054
2013	N-slope	192	10.88	9.57	906
	S-slope	192	10.99	9.32	929
2014	N-slope	189	11.14	9.78	978
	S-slope	158	11.05	9.48	987
2015	N-slope	195	12.09	8.81	1036
	S-slope	196	12.18	9.59	1062
Mean (\pm SD)	N-slope	180 \pm 20	11.3 \pm 0.4	9.5 \pm 0.4	985 \pm 50
	S-slope	178 \pm 16	11.4 \pm 0.5	9.6 \pm 0.2	1008 \pm 54

225 **3.2 Nutrient content in soil and foliage**

226 Soils at both sites were strongly acid with low CEC, P content and plant-available base cations except for K (Fig. 3, Table
 227 S2). The concentrations of base cations were systematically higher on the N-slope than on the S-slope. Statistically
 228 significant differences were detected for CEC and Mg (Fig. 3). The concentration of Ca was below the detection limit for
 229 half of the samples. The content of Cox and N was high, with a favourable C/N ratio at both sites.

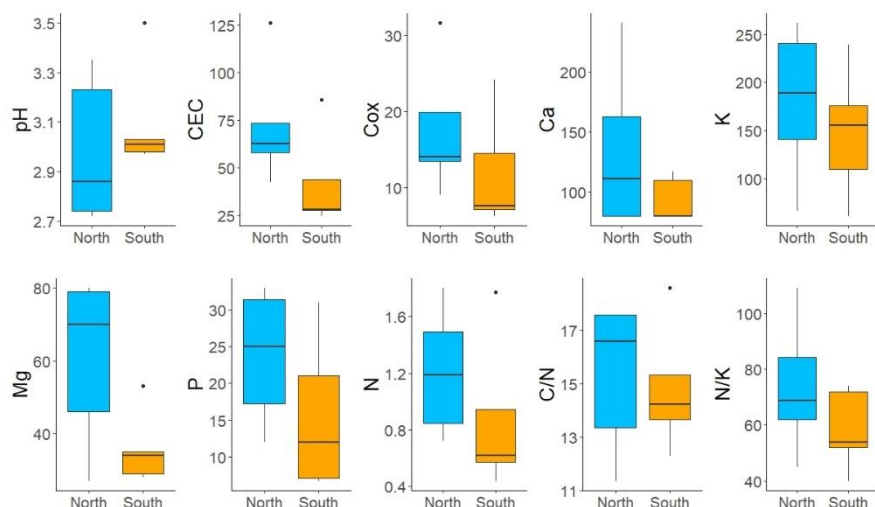
230 In line with soil nutrient analysis, foliar macroelements were higher on the N-slope than on the S-slope both in current- and
 231 previous-year needles (Table 2). For the current-year needles, the concentrations of base cations (Ca, K, Mg) were about 25-
 232 29% higher on the N-slope. The content of P and N was also substantially (16-21%) higher on the N-slope (Table 2).

233

234 **Table 2: Foliar nutrients in mg/kg of dry matter. Samples were pooled from six trees at each site.**

Sample	Ca	K	Mg	P	N _{total}	S _{total}
N-slope current year	3944	7059	1177	1456	1.54	1040
S-slope current year	2785	5248	849	1213	1.32	833
N-slope previous year	4954	5913	1064	1245	1.64	1125
S-slope previous year	4608	4650	898	1039	1.31	887

235



236

237 **Figure 3: Differences in soil characteristics between south- (orange) and north-facing (blue) slopes. Variables: exchangeable pH,**
238 **cation exchange capacity (CEC) (mol+/100g), soil organic carbon (Cox) (%), plant-available concentrations of Ca, Mg, K, P with**
239 **Mehlich III extraction solution (mg/kg), total soil N (%), and ratios of C/N and N/K. The analytical results for Ca that were below**
240 **the detection limit were replaced by 4/5 of the detection limit.**

241 3.3 Wood formation

242 The N-slope exhibited a higher number of newly formed cells each year, with the greatest difference compared to the S-slope
243 found in 2014 (Fig. 4, Fig. S2). Although the difference was systematic across years and all parts of the growing season, it
244 was statistically non-significant due to the limited number of sampled trees and natural between-tree variability in
245 xylogenesis. The higher number of cells on the N-slope resulted from consistently higher mean and maximum cell formation
246 rates, i.e., faster stem growth; the difference was statistically significant in 2014 ($p < 0.05$) (Fig. 4, Fig. S3). Note that while
247 the tree age distribution was comparable between sites in 2012 and 2014, trees on the N-slope were about 50 years older in
248 2013 (Table S1). The higher cell formation rates at the N-slope were consistent with significantly higher mean basal area
249 increments at the N-slope compared to S-slope considering the entire lifespan of trees (Fig. S4).

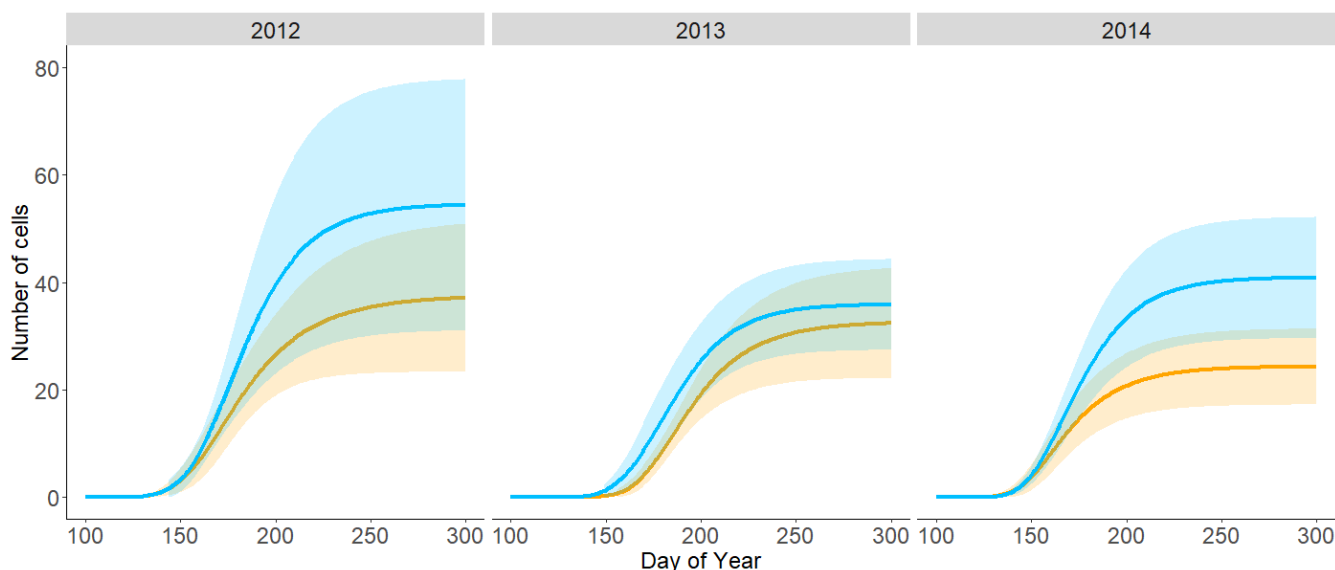
250 Critical dates of wood formation, such as dates of the beginning, peak and end of wood formation did not show any
251 consistent pattern, and no difference was statistically significant (Fig. S3). The variability in critical dates among trees on the
252 S-slope was usually higher than on the N-slope. Similar to critical dates derived from the Gompertz equation, there were no
253 consistent differences in dates of cell phenological phases between sites based on raw cell development data (Fig. S5). It is
254 worth mentioning that the duration of cell wall thickening was significantly longer on the N-slope in 2013 and 2014.

255 Logistic regressions with growth resumption indicated by the first enlarging cells (binary response variable) and soil
256 temperature (predictor) better fitted the data than regressions with cambial division (active/inactive - binary response
257 variable) and air temperature (predictor) (Fig. S6). Growth onset represented by the occurrence of the first cambial cells
258 occurred at 3.3 and 3.9 °C soil temperature and 3.6°C and 4.5°C air temperature on the S-slope and N-slope, respectively. In



259 contrast, thresholds for the first enlarging cells were very similar at both sites and occurred at 4.7 °C of soil temperature at
260 both sites and 6.4°C and 6.3°C of air temperature on the S-slope and N-slope, respectively.

261



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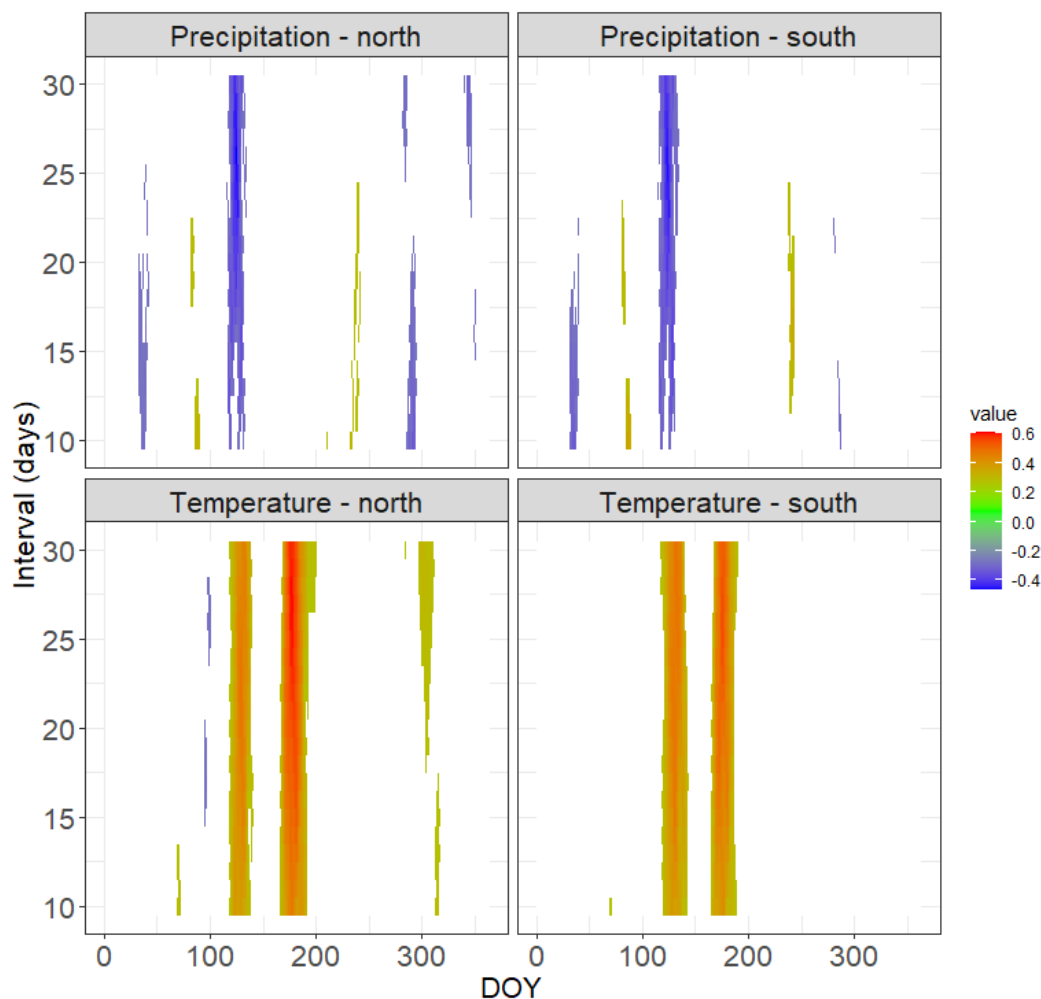
263 **Figure 4: Number of tracheids in the newly developing annual tree ring for 2012-2014 for the north- (blue) and the south-facing**
264 **(orange) site. Graphs show data fitted by the Gompertz function. Buffers denote 95 % confidence intervals.**

265

266 3.4 Climate response of tree-ring width chronologies

267 Both sites showed two prominent periods with significant temperature-growth correlations, potentially indicating crucial
268 parts of the season for annual ring width formation – the beginning of the growing season centered around DOY 125 (first
269 week of May) and the peak growing season centered around DOY 180 (end of June, Fig. 5). Positive temperature-growth
270 correlations were slightly stronger on the N-slope, with the maximum correlation coefficient exceeding 0.6 for a 25-day
271 period centered around DOY 179. There was a significant negative correlation of growth at both sites with precipitation
272 centered around DOY 115-125, which overlaps the positive effect of temperature at the beginning of the growing season
273 (Fig. 5). The remaining significant climate-growth correlations are restricted to very short periods and might be stochastic.

274



275

276 **Figure 5: Climate-growth correlations for tree-ring width chronologies of the north and south-facing site calculated over the**
277 **period 1961-2013. Only statistically significant correlations are shown, and the time window is centred over the respective days of**
278 **the year (DOY). The y-axis shows the length of the window of the number of consecutive days for which the correlations were**
279 **computed. Tree-ring chronologies are shown in Fig. S7.**

280 **4 Discussion**

281 We present a study that combines observations of radial stem growth at weekly temporal resolution with the analysis of sub-
282 daily local microclimate and site nutrient availability at cold sites located at the lower part of the treeline ecotone about 150
283 m below local tree maxima. We found that phenological dates, particularly the onset of wood formation, as well as radial
284 growth in relative terms, were strongly temperature-limited at both sites as expected, but the absolute growth rate was
285 systematically higher on the N-slope than on the S-slope. This is in line with our finding that soils were considerably richer
286 in nutrients on the N-slope, which was also warmer than the S-slope during the nighttime.



287

288 **4.1 Thermal and nutrient limitation of growth in the lower part of the treeline ecotone**

289 We expected to find either the same thermal conditions within tree patches on both slopes or a slightly warmer S-slope
290 (Paulsen et al., 2001), leading to similar growth onset, duration, and a similar growth rate. However, while we did find that
291 both sites showed similar thermal conditions and thus similar constraints and timing of beginning and peak growth phases,
292 the N-slope exhibited a systematically higher seasonal growth rate, albeit significant only in 2014. Consistently, significantly
293 higher basal area increments were observed for trees growing on the N-slope than on the S-slope.

294 So far, tree growth at cold sites has been considered predominantly as low temperature-limited (Babst et al., 2019).
295 Accordingly, we found clear support for the thermal limitation hypothesis as our temperature thresholds for growth
296 resumption were very similar at both sites (between 3.3°C and 6.4°C depending on the temperature variable) and similar to
297 the values published elsewhere (Rossi et al., 2007; Körner, 2021). Furthermore, radial stem growth at both sites, expressed as
298 annual tree-ring width, showed very high sensitivity to variations in temperature during the identical periods of the year:
299 Ring-width chronologies correlated with temperature mainly during the beginning of the growing season in early May,
300 which is indicative for the onset of growth in the early growing season (Castagneri et al., 2017; Carrer et al., 2017). The
301 second period with a significantly positive response of radial growth to temperature is the peak growing season at the end of
302 June, when the rates of cell division and enlargement culminate (Castagneri et al., 2017; Rossi et al., 2006b). Our data thus
303 show, in line with current knowledge, that the growing season at cold sites is strongly constrained by temperature, especially
304 regarding the timing of growth resumption and the timing of the peak rate of cell production during the growing season.

305 Notably, irrespective of the similar thermal constraints of stem growth on both slopes, the absolute production rate of new
306 tracheids was systematically higher on the N-slope. Differences between sites were not significant at the 5% probability level
307 except 2014, probably due to the limited number of sampled trees, though similar or higher in our study than what is a
308 common standard in wood formation studies (Cuny et al., 2015; Huang et al., 2021). Cell counts were systematically higher
309 each year on the N-slope, consistent with significantly higher stem growth over the entire lifespan of trees on the N-slope
310 compared to the S-slope (Fig S5). Factors responsible for the observed differences in growth rate could generally include
311 differences in microclimate, tree age and size (Rathgeber et al., 2011; Zeng et al., 2017) or accessibility of nutrients. Tree
312 age was not significantly different between sites in 2012 and 2014 (the years with the greatest differences in cell counts). In
313 2013, trees were significantly older on the N-slope than on the S-slope, which should be expressed in a lower number of
314 cells per tree ring on the N-slope due to the age trend in cell number (Lundqvist et al., 2018). However, we observed the
315 opposite pattern.

316 It is unclear to what extent microclimatic differences were decisive in our study since we found between-site thermal
317 differences within or close to the measurement error of the thermistors. The S-slope tended to be slightly more favourable
318 with respect to air temperature and degree day sums. However, the N-slope was warmer during the night when stem water
319 potentials are highest with intense cell expansion and division (Zweifel et al., 2021), which may thus benefit stem growth



320 there. Differences in soil temperature were ambiguous: the S-slope tended to be warmer than the N-slope at the beginning of
321 the growing season, but the N-slope was warmer during the peak growing season, leading to slightly warmer soils on N-
322 slope for the June-September period. Only in the warmest year of the measurement period (2015), the S-slope was
323 substantially warmer.

324 Overall, our temperature measurements showed that a part of the growing season was characterized by air and soil
325 temperature well above the growth-limiting threshold of $>5^{\circ}\text{C}$ (Körner, 2021), potentially allowing for the influence of other
326 growth-limiting factors. One plausible explanation for the observed growth differences could thus be nutrient availability.
327 Specifically, we assume the better growth performance of trees at the N-slope may be due to a higher availability of base
328 cations and perhaps also P, as can be seen from nutrient concentrations measured both in soils and in needles. Higher
329 concentrations of leaf macronutrients at N-slope could potentially indicate greater sink limit of growth (Hoch and Körner,
330 2012; Fajardo and Piper, 2017). However, in the light of higher growth rates and concentrations of macronutrients in soils of
331 the N-slope, we interpret this pattern as a consequence of higher uptake of nutrients reflected in the source-driven higher
332 growth rate (Ellison et al., 2019). Our findings underscore the critical role of nutrients on the growth rate and above-ground
333 biomass production (Dobbertin, 2005; Li et al., 2018; Oulehle et al., 2023).

334 Not surprisingly, in an ecosystem saturated with N (Novotný et al., 2018), the main between-site differences cannot be
335 attributed to N availability but to other nutrients such as Ca, Mg, or P. This applies especially to very acid soils with a pH of
336 around 3, as in our case, where leaching of basal cations is likely (Lucas et al., 2011). In environments rich in C and N,
337 stoichiometric requirements for building new biomass make other nutrients limiting, especially base cations and P (Mellert
338 and Ewald, 2014; Norby et al., 2022; Körner, 2022). So far, most studies accentuated N availability as an important
339 constraint of the growth performance of trees at cold sites (Möhl et al., 2018; Gustafson et al., 2021), but these studies
340 focused on ecosystems not saturated with N. The important role of P for tree growth has also been shown in forest
341 ecosystems near their cold margin (Hagedorn et al., 2020; Ellison et al., 2019). Consistent with the traditional Liebig's law
342 of the minimum (Liebig, 1840), our study highlights the importance of general stoichiometric principles of nutrient
343 requirements for the production of new biomass, which may also play a crucial role in the growth rate of trees at cold sites.

344 The source of the higher nutrient content in soils of our N-slope is not entirely clear. Metamorphic rocks prevalent on the
345 north-facing slope are generally richer in Mg, Ca and K than granites prevalent on the S-slope, while the content of P is
346 comparable between metamorphites and granites (Czech Geological Survey, 2024). Additionally to weathering, higher
347 nighttime temperatures and slightly higher soil temperatures in the peak growing season on the N-slope may have enhanced
348 decomposition rates and thus indirectly growth performance. Similar relationships between higher soil temperatures, higher
349 soil nutrient content, and enhanced tree growth have been suggested for subarctic treeline ecotones (Sullivan et al., 2015;
350 Dial et al., 2024).

351



352 4.2 Implications for tree growth in topographically complex cold landscapes

353 Our data generally support the idea that the thermal differences between high-elevation slopes under forest cover are
354 relatively subtle in the temperate zone (Paulsen and Körner, 2001; Treml and Banaš, 2008, Rita et al., 2021). Additionally,
355 we would like to highlight two striking patterns related to our N-slope and S-slope sites that may be generalizable. First, the
356 duration of direct sunlight during the growing season was longer on the N-slope, probably due to incoming morning and
357 evening sunlight from the northeast and northwest, respectively. This phenomenon might increase with increasing latitudes
358 and be stronger at less steeper slopes. An extreme example is the midnight irradiation of north-facing slopes beyond the
359 polar circle (Kirchhefer, 2000). Second, probably as a consequence, nighttime air temperature was higher on the N-slope
360 compared to the S-slope, leading to equal mean daily air temperature on both sites (the S-slope was warmer during the
361 warmest part of the day). However, since the differences in night temperature were rather high, topographical effects on local
362 air masses ventilation resulting in relatively lower radiative cooling on the N-slope than on the S-slope should also be
363 considered in our case (Barry et al., 1992). Higher nighttime air temperature on the N-slope may also be the cause of warmer
364 soils in some years but with differences close to the measurement error. We conclude that the thermal differences between
365 tree stands growing on supposedly warmer, more growth-favorable south-facing slopes and cooler north-facing slopes are so
366 subtle that they may be overridden by local topography with related relief shading and local circulation.
367 Faster growth of trees on soils richer in nutrients also implies that the advance of current upper tree limits, which lag behind
368 the pace of warming (Körner and Hiltbrunner 2024), might be faster on fertile soils because seedlings could potentially reach
369 a mature and reproductive age earlier (Dial et al., 2022). This remains to be rigorously tested, although some studies have
370 already suggested greater potential for treeline advancement on fertile soils (Rousi et al., 2018; Gustafson et al., 2021).

371

372 Conclusions

373 We demonstrated that in the lower part of treeline ecotone of temperate mountains, thermal differences between tree stands
374 growing on supposedly warmer, more growth-favorable south-facing slopes and cooler north-facing slopes are subtle and
375 may be overridden by relief shading and local air circulation. Crucial phases of stem growth, particularly the onset of wood
376 formation and timing of peak growth rate, were constrained by temperature and day length. However, the absolute growth
377 rate was systematically higher on the N-slope with soils considerably richer in nutrients. Our results advocate for a joint
378 effect of nutrient-driven absolute growth rate together with the thermally constrained growth phenology at sites close to the
379 cold range limit of trees. The effect of nutrient availability can be superior to the effect of slope aspect for absolute stem
380 growth rates of *Picea abies* in the lower parts of treeline ecotone. These findings are important for understanding of stem
381 growth trends at treelines which currently often lag behind the pace of warming.

382

383



384 **Data availability**

385 The data used for the analyses together with R scripts are available here: [10.5281/zenodo.14619874](https://zenodo.org/doi/10.5281/zenodo.14619874)

386 **Supplement**

387 This article is accompanied by supplementary material.

388

389 **Author contributions**

390 HK and VT conceptualized the study. HK, and VT performed data processing. TCh and JT contributed to data analyses. HK
391 and VT lead the paper writing. JL, TCh and JT contributed to paper writing (comments and revisions).

392

393 **Competing interests**

394 The authors declare no competing interests.

395 **Special issue statement**

396 This article is part of the special issue “Treeline ecotones under global change: linking spatial patterns to ecological
397 processes”.

398 **Acknowledgements**

399 We appreciate the authority of the Krkonoše National Park for the permission to conduct research and for the logistical
400 support. We further thank Jakub Kašpar and Šárka Zákřavská for their help with fieldwork.

401 **Financial support**

402 This study was funded by the Czech Science Foundation, grant number 22-26519S. H.K., V.T., J.L. and J.T. were supported
403 by the Johannes Amos Comenius Programme (P JAC), project No. CZ.02.01.01/00/22_008/0004605, Natural and
404 anthropogenic georisks.

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