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This is the author's manuscript

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1678981> since 2021-12-09T16:31:25Z

Published version:

DOI:10.1111/1365-2745.13073

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(Article begins on next page)

1 **Twelve years of low nutrient input stimulates growth of trees and dwarf shrubs in**
2 **the treeline ecotone**

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24

25 Running headline:

26 Nutrient addition stimulates growth at treeline

27

28 **Abstract**

29 1. Almost all natural terrestrial ecosystems are nutrient limited in terms of growth,
30 and we expect treeline vegetation to be no exception. However, direct constraints of
31 low temperature on tissue formation may superimpose effects of low nutrient
32 availability.

33 2. We examined growth responses of two tree (*Larix decidua* and *Pinus uncinata*) and
34 two dwarf shrub species (*Vaccinium myrtillus* and *Vaccinium gaultherioides*) to 12
35 years of moderate fertilizer addition (NPK applied at a rate of 15 and 30 kg nitrogen
36 ha⁻¹ a⁻¹) along an elevation gradient within the treeline ecotone in the Swiss Alps
37 (2083 to 2225 m a.s.l.). We measured annual top- and side-shoot increments as well
38 as stem ring width in trees and shoot increments in dwarf shrubs.

39 3. Fertilizer addition increased soil nutrient availability, indicated by enhanced soil
40 extractable N, higher concentrations of N, P and K in leaves, and higher foliar $\delta^{15}\text{N}$.

41 4. Fertilizer addition stimulated annual growth of all four species: by 11–20% for *L.*
42 *decidua* and 15–36% for *P. uncinata* (depending on trait), and by 8–16% for the two
43 dwarf shrub species. Growth stimulation by the higher fertilizer dose was not
44 significantly stronger than by the lower dose (except for *V. gaultherioides*),

45 suggesting an overall low nutrient demand for growth and saturation at a rather low
46 nutrient input.

47 5. *Synthesis*. Even slightly enhanced nutrient availability can stimulate growth of trees
48 and dwarf shrubs in an alpine treeline ecosystem. Ongoing atmospheric nutrient
49 deposition, in conjunction with global warming, may accelerate plant growth at the
50 treeline.

51

52 KEYWORDS

53 fertilizer addition, *Larix decidua*, nitrogen isotope, *Pinus uncinata*, tree ring, shoot
54 length, Swiss Alps, *Vaccinium gaultherioides*, *Vaccinium myrtillus*

55

56 **Introduction**

57 Globally, the availability of nitrogen (N) and phosphorus (P) is considered to be a
58 major factor limiting growth and productivity in terrestrial ecosystems (Vitousek &
59 Howarth 1991). In recent decades, N availability for plants has increased in many
60 areas owing to atmospheric deposition of nitrogenous compounds (Vitousek et al.
61 1997; Galloway et al. 2008). In addition, global warming is expected to increase
62 turnover rates of soil organic matter (Kirschbaum 1995; Saxe et al. 2001; Kammer et
63 al. 2009; Bai et al. 2013; Dawes et al. 2017b), possibly enhancing the availability of
64 nutrients in general.

65

66 Arctic and alpine regions are expected to be especially low in plant-available nutrients
67 because of temperature constraints on decomposition and mineralization processes in

68 the soil (Körner 2003). Nitrogen availability generally decreases with an elevation-
69 associated decline in temperature (Loomis et al. 2006 [arctic mountain ranges];
70 Thébault et al. 2014; Fajardo & Piper 2017 [Andes]; Solly et al. 2017a [Ural]).
71 Substantial growth stimulation in response to fertilization has been observed for arctic
72 and alpine ground-layer plants (e.g. Schächli & Körner 1996; Van Wijk 2004; Bassin
73 et al. 2012). Even the vegetation of glacier forefields shows dramatic increases in
74 biomass production when nutrients are added (Heer & Körner 2002). Thus, growth in
75 cold ecosystems makes no exception to the general nutrient limitation of terrestrial
76 ecosystems.

77

78 Growth responses to an improved nutrient supply, however, often differ among plant
79 species and growth forms (e.g. Chapin et al. 1995; Thomas et al. 1999; Bassin et al.
80 2007; Klanderud 2008), mainly depending on a species' inherent ability to benefit
81 from additional nutrients and the degree to which growth is limited by factors other
82 than nutrient availability, such as temperature. Treelines follow a common isotherm at
83 5–7 °C (6.4 °C; Paulsen & Körner 2014) globally, suggesting that temperature limits
84 tree growth at and above the treeline (Körner & Paulsen 2004). Because tree canopies
85 are aerodynamically open to convective heat transfer (wind) and also shade the
86 ground (causing reduced soil heat flux), they experience colder conditions than low-
87 stature plants (including tree seedlings), which often profit from warmer
88 microclimates (Scherrer & Körner 2010; Körner 2012). Growth chamber experiments
89 have demonstrated that growth of juvenile trees is greatly reduced at temperatures
90 below ca. 6 °C, even under an optimal nutrient supply (Iivonen et al. 1998; Alvarez-
91 Uria & Körner 2007; Hoch 2013; Ferrari et al. 2016). This suggests that the growth

92 responses to nutrient addition can be strongly constrained under critically low
93 temperatures.

94

95 Globally, soil types and thus fertility vary considerably among treelines, indicating
96 that nutrient availability does not consistently affect treeline position the way growing
97 season temperature does (Körner 2012). While low nutrient availability may not be
98 decisive for the establishment of seedlings, it may constrain the vigor of saplings and
99 trees. However, a global assessment of foliar N concentrations in herbs and trees has
100 demonstrated an increasing rather than a decreasing trend with increasing elevation
101 (Körner 1989). Hence, tree life at high elevations is not associated with an obvious
102 foliar nutrient deficiency. Accordingly, the needle N concentration of *Picea abies* and
103 *Pinus cembra* does not change over the uppermost ca. 300 m of elevation in the Swiss
104 Alps, although growth rate declines substantially (Birmann & Körner 2009). On the
105 other hand, fertilizer addition experiments have reported growth responses of treeline
106 trees to fertilization, similar to responses observed for other vegetation (see above).
107 This indicates that trees in cold climates make no exception in taking advantage of
108 added nutrients in terms of growth. Within three years of a single, high dose
109 application of NPK (85–175 kg N ha⁻¹), growth of *Betula pubescens* was found to
110 respond more strongly at the treeline compared with two lower sites in northern
111 Sweden (Sveinbjörnsson 1992). At the Finnish arctic treeline, 50-year-old *Pinus*
112 *sylvestris* showed a tripling of annual growth in response to ca. 150 kg N ha⁻¹ a⁻¹ of
113 NPK (Susiluoto et al. 2010). Sullivan et al. (2015) presented various lines of
114 observational evidence (no nutrients added) suggesting that growth of arctic treeline
115 trees in Alaska is predominantly limited by nutrients.

116

117 Here, we present results from a 12-year low-dose fertilization experiment at a treeline
118 in the Swiss Alps. Over an elevation gradient of 140 m across an afforestation site in
119 the current treeline ecotone, we annually added NPK fertilizer corresponding to 15 or
120 30 kg N ha⁻¹ a⁻¹ to plots containing 30-year-old (in the first year of fertilization) *Larix*
121 *decidua* or 32-year old *Pinus uncinata* individuals with an understory of mainly
122 ericaceous dwarf shrubs. To quantify growth, we measured annual shoot increments
123 of trees and dwarf shrubs as well as stem ring width of trees. We also measured
124 nutrient concentrations in the soil and assessed the foliar nutritional status of trees and
125 dwarf shrubs. While the very high fertilizer doses used in previous studies (see above)
126 may have prevented competition effects between trees and understory vegetation, we
127 used doses not uncommon in the front ranges of the Alps to provide more realistic
128 insight into growth responses to anthropogenic increases in nutrient availability.
129 Atmospheric N deposition in the inner parts of the Alps is mostly below 20 kg N ha⁻¹
130 a⁻¹ (e.g. Hiltbrunner et al. 2005, Rogora et al. 2016) and empirically defined
131 thresholds for measurable long-term effects on ecosystems (so called 'critical loads',
132 Nilsson 1988) are in the range of 5–15 kg N ha⁻¹ a⁻¹ for comparable ecosystems, such
133 as coniferous woodland and alpine shrub habitats (Bobbink & Hettelingh 2010). The
134 estimated background deposition of ca. 4–8 kg N ha⁻¹ a⁻¹ in our test region (Rihm &
135 Kurz 2001, Schmitt et al. 2005) may already have exerted some growth stimulation,
136 and we expected that a doubling or tripling of such low rates would have clear effects.

137

138 We aimed to determine whether the growth stimulation observed in previous short-
139 term fertilization trials conducted at treeline locations occurs in a longer-term study,

140 and whether possible negative effects of nutrient addition offset the benefits of any
141 growth stimulation. Given the general sensitivity of plant growth to nutrient addition
142 in natural ecosystems, we expected (1) growth to be stimulated already by the lower
143 NPK-fertilizer dose corresponding to 15 kg N ha⁻¹ a⁻¹ and (2) growth stimulation to
144 differ between growth forms, with smaller effects of nutrient addition for trees than
145 for dwarf shrubs, as upright trees are exposed to lower temperatures. Further, we
146 expected (3) the effect of fertilization to vary across temperature gradients. On a
147 spatial scale, we predicted that the response would decrease with increasing elevation
148 within the treeline ecotone, owing to greater low temperature limitation of tissue
149 formation. On a temporal scale, we predicted larger responses to fertilization in
150 warmer years, when direct thermal constraints are relieved.

151

152 **Materials and methods**

153 **STUDY SITE**

154 The experiment was located within a 5 ha long-term afforestation site in the temperate
155 continental climate zone of the inner Alps (Stillberg, Davos, Switzerland; 46°47'N,
156 9°52'E). In 1975, more than 92,000 tree seedlings of *Larix decidua* Mill., *Pinus mugo*
157 ssp. *uncinata* [DC.] Domin (referred to hereafter as *P. uncinata*) and *Pinus cembra* L.
158 were planted into the intact dwarf shrub heath (Kuoch 1970), slightly above the
159 treeline in the region (Barbeito et al. 2012). The afforestation site was partitioned into
160 plantation quadrats 12.25 m² in area, each containing 25 evenly spaced individuals
161 (Supporting Information, Fig. S1). From 1975 to 2005, vertical growth of all three
162 tree species decreased substantially with increasing elevation (Barbeito et al. 2012).
163 At the beginning of our study, tree height declined from ca. 3.2 m to 1.4 m in larch

164 and from 1.6 m to 1.0 m in pine across the elevation range of 142 m (2083 to 2225 m
165 a.s.l.) covered in the present experiment (Fig. S2). On-site climate data is available
166 from a weather station situated at the lower end of the site (2090 m a.s.l.). On average,
167 annual precipitation was 1159 mm and annual mean temperature was 2.0 °C over the
168 last 40 years (1975 to 2015). January is the coldest and July the warmest month, with
169 mean temperatures of -5.4 °C and 10.2 °C, respectively. The growing season lasts 3–4
170 months (June to September) at this location. A second weather station on the same
171 slope at 2220 m. a.s.l. suggested a lapse rate of 0.55 K per 100 m of elevation for the
172 summer months of 2011 and 2012. A 30-year comparison of summer temperatures
173 measured on site and those measured at a weather station 8 km away at 2691 m a.s.l.
174 suggested a lower lapse rate of ca. 0.48 K per 100 m of elevation. Thus, we expect
175 that our experimental site covered a mean air temperature gradient of at least 0.7 K in
176 a temperature range considered critical for tree growth. Date of snowmelt (Barbeito et
177 al. 2012) and freezing events (Rixen et al. 2012) are important modulating factors for
178 growth at the study site.

179

180 The most common understory plants at the site are the ericaceous dwarf shrubs
181 *Vaccinium myrtillus* L., *Vaccinium gaultherioides* Bigelow (group *V. uliginosum*
182 aggr.) and *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher, reflecting the
183 oligotrophic nature of these ecosystems. Soils are acidic (pH 3.5 to 4.5), developed on
184 siliceous bedrock (Schönenberger & Frey 1988) and have a sandy texture. Soil types
185 at the afforestation site vary with microtopography, with rankers on the ridges and
186 iron-humus podzols within gullies. All soils have 5 to 20 cm thick mor-type organic
187 layers (Bednorz et al. 2000). Detailed descriptions of soil and microclimatic

188 conditions at the site can be found in Blaser (1980), Bednorz et al (2000),
189 Schöenberg & Senn (2001) and Hagedorn et al. (2010).

190

191 EXPERIMENTAL DESIGN

192 We chose 22 locations throughout the afforestation site (Fig. S1), hereafter referred to
193 as blocks, that covered the whole range of micro-environmental conditions (see Senn
194 & Schöenberger 2001). Half of the blocks included European larch (*L. decidua*) and
195 the other half included mountain pine (*P. uncinata*). Within each block, we randomly
196 selected three plantation quadrats as experimental plots. Each plot was assigned to a
197 control (no fertilization) or to one of two fertilizer dose treatments. Treatments were
198 assigned randomly but confined so that the location of fertilized plots within a block
199 was not directly above control plots to avoid nutrient input from drainage. The
200 elevation difference between treatment plots of the same block was 5.4 ± 0.7 m (mean
201 \pm SE). We annually applied the mid- to long-term fertilizer ARBOSTAR
202 (N:P₂O₅:K₂O:Mg = 8:4:11:2; Geistlich Arbostar, HBG Düngevertrieb AG,
203 Grossaffoltern, Switzerland) at an amount that corresponded to 15 kg N ha⁻¹
204 ('NPK15') or 30 kg N ha⁻¹ ('NPK30'). About 75% of the N in the fertilizer was in the
205 form of NH₄⁺ and the rest was derived from methylene urea. Fertilizer was first
206 applied in September 2004 and then at the beginning (June) of each following
207 growing season until 2016. Fertilizer granules were evenly distributed by hand over
208 the entire area of a given plot.

209

210 SOIL ANALYSES

211 Six soil cores (0–10 cm depth, 5 cm diameter) per plot were collected in September
212 2010. Soil samples were bulked plot-wise and sieved at 4 mm mesh size, and fine
213 roots were removed. Subsequently, samples were stored at -20 °C until chemical
214 analysis. For analyses of soil inorganic N, an aliquot of 20 g of soil was extracted
215 with 100 ml of 0.5 M K₂SO₄, following the protocol of Brooks et al. (1996). The
216 ammonium concentration in the extracts was determined colorimetrically by
217 automated flow injection analysis (RF-535 Fluorescence HPLC Monitor, Shimadzu).
218 The nitrate concentration (NO₃⁻) was measured colorimetrically according to Navone
219 (1964).

220

221 For the analysis of stable isotope ratios, soil aliquots were dried at 60 °C, milled and
222 then analysed using an automated elemental analyser (Euro EA 3000, HEKAtech,
223 Wegberg, Germany) interfaced with a continuous flow isotope ratio mass
224 spectrometer (Delta-S, Thermo Finnigan, Bremen, Germany). The ¹⁵N natural
225 abundance in extracted NH₄⁺ was determined by the diffusion technique (Schleppi et
226 al. 2006), converting NH₄⁺ to NH₃ and trapping it on acidified teflon filters. The
227 filters were packed in tin (Sn) capsules and then measured immediately by mass
228 spectrometry. The pH of the bulk soil was measured potentiometrically in H₂O at a
229 soil-to-solution volume ratio of 1:2.5.

230

231 PLANT RESPONSES

232 In late August of 2010 and 2016, 20–25 new needles were sampled from three (2010)
233 to five (2016) randomly chosen trees (larch or pine) per plot. The same number of

234 leaves was collected from roughly 10 branchlets per plot for each of the two dominant
235 dwarf shrubs *V. myrtillus* and *V. gaultherioides*. Needles were sampled from the
236 upper canopy on the south side of the trees. Leaves from dwarf shrubs were sampled
237 from the upper shrub canopy, thus avoiding deep shade. Samples were dried at 65 °C
238 for 24 hours, milled to a fine powder and weighed into tin capsules (1–2 mg per
239 sample). Nitrogen per dry mass and $\delta^{15}\text{N}$ were obtained by mass spectrometry in
240 connection with an element analyser, as described for the soil samples. In 2010, we
241 additionally determined phosphorus (P), potassium (K) and magnesium (Mg)
242 concentrations of leaf samples. Phosphorus concentrations were analysed
243 photometrically using an UV-VIS spectrometer (UV-160A, Shimadzu Europe GmbH,
244 Germany; DIN EN ISO15681-1). Potassium and Mg were determined by atomic
245 flame spectrometry (SpectrAA 220, Varian Deutschland GmbH, 64289 Darmstadt,
246 Germany; DIN EN ISO 9964-2 for K and DIN EN ISO7980 for Mg).

247

248 In 2004, we selected three census trees in each plot that were visibly unaffected by
249 frost damage or snow fungus and were not heavily shaded by surrounding trees. Tree
250 and shrub growth was measured in 8 years from 2004 (pre-treatment year) to 2016.
251 No measurements were made from 2011 to 2015. During this period, several of the
252 originally selected trees died, were damaged or lost their labels, prompting us to select
253 new trees for the final census in 2016 using the original criteria. There was no
254 difference in tree ring width between the trees selected in 2004 and the trees selected
255 in 2016 in four overlapping years (2007 to 2010, see Fig. S3). Thus, we are confident
256 that selecting new trees did not have a qualitative effect on the results. In 2005 and
257 2015, the survival status (alive or dead) of all trees growing on the afforestation site

258 was documented, allowing us to investigate the influence of the treatment on tree
259 mortality.

260

261 For the annual growth census, one branch per tree at approx. half the tree height was
262 marked to assess side-shoot growth. We obtained tree shoot increment data for 2004
263 to 2016 using obvious annual bud scars/branching nodes. The increment of top- and
264 side-shoots in 2007 and 2009 and from 2011 to 2015 was back-measured in the
265 subsequent years. Top-shoot increment of larch was not measured in 2009 and 2010.

266

267 In 2010 and 2016 we collected microcores (35 mm length, 2 mm diameter) from all
268 marked trees using an increment puncher (Trephor, Università degli Studi di Padova,
269 S. Voto di Cadore, Italy). Cores were extracted from two sides of the main stem (east
270 and west in 2010 and north and west in 2016), above the curved section at the stem
271 base, at a height of roughly 20–40 cm for pine and 60–100 cm for larch. After
272 extraction, the cores were stored in 80% ethanol and later dried at room temperature
273 for 10–12 hours before measuring ring width. We cut the cores lengthwise, applied
274 chalk powder to the cut surface to improve the visibility of the growth rings, and
275 measured ring width with a stereomicroscope at 40x magnification. Ring width of the
276 two cores per tree were averaged prior to statistical analysis. For each tree surveyed in
277 2016, we additionally measured total tree height as well as tree diameter at two
278 heights (roughly 20 and 80 cm above ground level for larch and 20 and 40 cm for
279 pine), which we averaged for statistical analysis.

280

281 For the dwarf shrubs, the annual increments of the longest shoot of five randomly
282 chosen branchlets per species were measured in each plot from 2004 to 2010. The
283 annual increment formed in 2007 (*V. myrtillus* only) and 2009 was back-measured in
284 the subsequent year (2008, 2010). Increments from 2013 to 2016 were measured in
285 2016, but we have no data for 2011 to 2013 because increments older than two years
286 could not be clearly identified. In 2016, we measured the longest shoots of only three
287 randomly chosen ramets (instead of five) per species. Shoot increments were always
288 measured in autumn after annual growth was complete.

289

290 STATISTICAL ANALYSES

291 We assessed the effects of fertilizer addition, other explanatory variables (treatment
292 year; plot elevation; tree species in the plot [in shrub models]) and their potential two-
293 way interactions with fertilization on measured soil properties and plant traits.
294 Specifically, we fitted linear mixed-effects models in R version 3.4.1 (R Core Team
295 2017) using the lme function of the nlme-package by Pinheiro et al. (2016). The
296 fertilizer dose (control, NPK15, NPK30) and treatment year (2005–2016) were
297 generally analysed as categorical variables (factors), whereas elevation was analysed
298 as a numerical variable (2083 to 2225 m a.s.l.). This approach resulted in separate,
299 unbiased coefficients for each level of fertilizer dose and year, which were used to
300 create Figures 3 and 4. The models for foliar nutrient concentration and nutrient ratios
301 indicated linear relationships between these traits and the fertilizer dose, prompting us
302 to rerun the model with fertilizer dose as a numeric variable (0, 15 or 30 kg N ha⁻¹ a⁻¹
303 ¹). We analysed annual growth traits separately for each species, whereas the other
304 response variables (foliar nutrient concentration and $\delta^{15}\text{N}$, diameter and height of

305 trees) were analysed with one model for both species of the same growth form. Data
306 from the pre-treatment year (2004) were tested separately for differences among
307 treatment groups. Tree mortality was investigated with logistic regression (glmmPQL
308 function) using survival data for the period between 2005 and 2015.

309

310 We included random intercepts for experimental block in all models (a total of 11
311 blocks per tree species and 22 per shrub species, see Fig. S1). As each of the blocks
312 contained three plots from which multiple samples were taken, we added plot identity
313 as a nested random effect within block. For repeatedly measured traits on the same
314 individual trees (top- and side-shoot increment, ring width), we also included tree
315 identity as a nested random effect within block and plot, thereby allowing the model
316 intercept to vary among trees. Further, we implemented an autocorrelation structure of
317 order 1 (corAR1 in nlme) in models with repeated measures to account for temporal
318 autocorrelation, which improved the AIC (Akaike information criterion) of the
319 models. We expected residual variance to differ between treatments, years and/or
320 species. Therefore, we allowed the residual variance to differ between levels of these
321 factors by using the varIdent function in nlme (Zuur et al. 2009). F-statistics and
322 detailed model specifications are given in the Supporting Information (Tables S3–S5).
323 Model assumptions of residual normality and homoscedasticity were verified visually
324 (q-q plot, Tukey-Anscombe plot) for each model. To improve residual spread in cases
325 of heteroscedasticity, the response variable was log or square root transformed
326 (Supporting Information, Table S1). Model estimates for each year and treatment
327 (averaged over all other factors in the model, as shown in Figures 2 and 3) were
328 obtained with the lsmeans package in R (Lenth 2016). Using the same package, we
329 calculated the average estimates across the twelve years (Table 1), performed t-tests

330 on contrasts between treatments and back-transformed the estimates for presentation.
331 Log-transformed values yield the geometric mean and square-root-transformed values
332 an intermediate between arithmetic and geometric mean when back-transformed.
333 Numerator degrees of freedom (df) are given for t-tests.

334

335 To test the influence of annual climatic conditions on the growth responses to
336 fertilization (i.e. control vs. fertilized plots), we combined the data from the two
337 fertilizer doses because there was no qualitative difference between the growth
338 responses to NPK15 and NPK30. The factor 'year' was replaced by number of frost
339 events per growing season and mean summer temperature (June, July and August
340 together) in the air (2 m above ground). The statistical significance of the resulting
341 trends was tested with t-tests and the corresponding *P*-values were corrected for
342 multiple testing using the 'Bonferroni-Holm' method. We considered the start and end
343 of the growing season as the dates when the daily mean soil temperature first rose
344 above or fell below 3.2 °C for two consecutive days, respectively (Körner and
345 Paulsen 2004, Dawes et al. 2011). Dates with daily minimum air temperatures
346 below -1 °C were considered as freezing events (Rixen et al. 2012). Freezing events
347 that spanned contiguous dates were counted only once. If not specified, results are
348 presented as treatment means with the corresponding 95% confidence intervals.

349

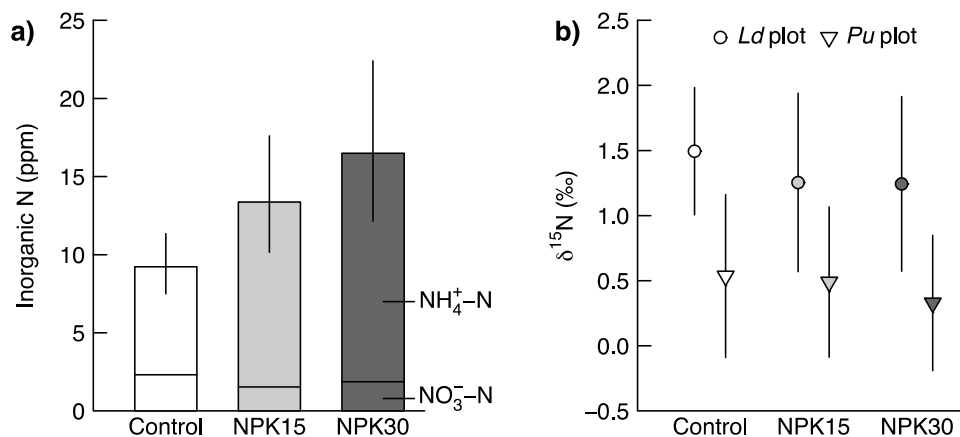
350 **Results**

351 TREATMENT EFFECTS ON SOIL PROPERTIES

352 In 2010, end-of-season inorganic N concentrations in the soil (0–10 cm depth)
353 increased by 45 [10, 90] % in NPK15 (df = 37, $t = 2.8$, $P < 0.01$) and 79 [32, 142] %

354 in NPK30 plots (Fig. 1; $df = 21$, $t = 3.9$, $P < 0.001$). The higher inorganic N
 355 concentrations were solely caused by an increase in NH_4^+ , which comprised ca. 75%
 356 of total inorganic N in control plots and 89% in the fertilized plots (Fig. 1). In
 357 contrast, the concentration of NO_3^- , which was not part of the fertilizer, remained
 358 unaffected in treated plots. NH_4^+ , but not NO_3^- , decreased significantly with
 359 increasing elevation, by ca. $0.77 [0.07, 1.46]$ mg N kg^{-1} per 10 m of elevation ($df =$
 360 37 , $t = 2.4$, $P = 0.021$). Elevation did not affect soil nutrient increases due to
 361 fertilization. There was a marginally significant trend of ca. 35% lower NH_4^+
 362 concentrations in plots with pine compared to in plots with larch ($df = 20$, $t = -1.8$, P
 363 $= 0.089$), independent of fertilization treatment.

364



365

366 **Figure 1** End of season inorganic N (a) and $\delta^{15}\text{N}$ (b) in the soil of control and fertilized plots,
 367 corresponding to 15 (NPK15) or 30 kg N ha^{-1} a^{-1} (NPK30), in 2010. Means and 95% confidence
 368 intervals are shown. a) Bars are subdivided for the fraction of inorganic N derived from ammonium
 369 (NH_4^+ -N) and nitrate (NO_3^- -N). b) Soils of plots containing either *Larix decidua* (*Ld*) or *Pinus uncinata*
 370 (*Pu*) differed in $\delta^{15}\text{N}$ and are displayed separately.

371

372 Bulk soil $\delta^{15}\text{N}$ was not significantly affected by fertilization (Fig. 1; fertilizer $\delta^{15}\text{N}$
373 was ca. 0.80 ‰). Similarly, $\delta^{15}\text{N}$ in soil extractable NH_4^+ was not significantly
374 affected by fertilization (control: 0.26 ‰, NPK15: 0.48 ‰, NPK30: 0.44 ‰). Soil
375 $\delta^{15}\text{N}$ signatures were significantly higher in plots with larch than in plots with pine
376 (Fig. 1; $df = 20$, $t = 2.9$, $P = 0.010$). The treatment did not affect the soil pH of 3.79
377 [3.72, 3.86].

378

379 FOLIAR NUTRIENT CONCENTRATIONS AND ISOTOPE RATIOS

380 Across treatments, foliar N concentration of larch decreased with elevation in 2010,
381 from 2.39 [2.22, 2.56] mg g^{-1} at the lowest elevation to 2.05 [1.94, 2.18] mg g^{-1} at the
382 highest elevation (Table S2). This decrease led to a parallel decrease of the N:P and
383 N:K ratios towards higher elevation for larch. However, this relationship between
384 foliar N and elevation disappeared in leaves sampled in 2016 (Table S2). For pine,
385 only the N:K ratio decreased from 3.57 [2.94, 4.34] at the lowest elevation to 2.08
386 [1.64, 2.63] at the highest elevation in 2010 (Table S2).

387

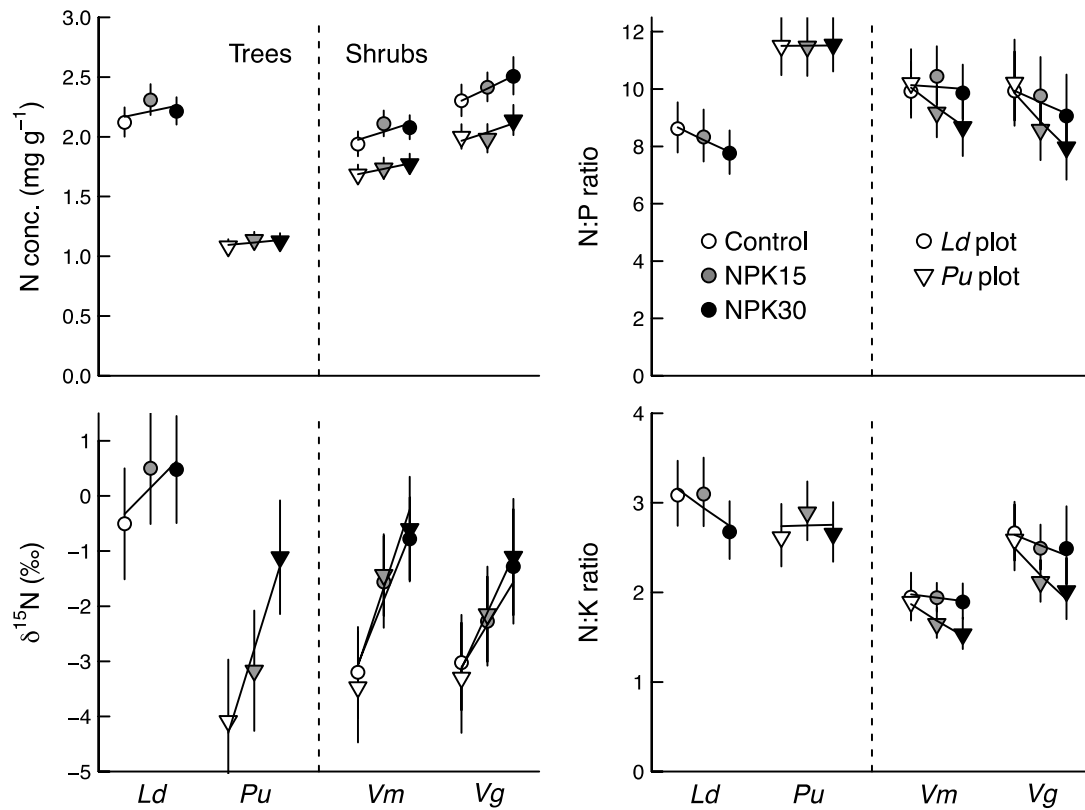
388 In 2010, no significant response to fertilization was found in foliar N concentration of
389 trees, except for a stimulation in larch when grown in the NPK15 treatment (Fig. 2; df
390 = 38, $t = 2.4$, $P = 0.024$). The second sampling in 2016 revealed a stronger and linear
391 response for both species, amounting to a maximum of +10% in the NPK30 treatment
392 ($df = 34$, $t = 3.4$, $P < 0.01$; Fig. S4). Phosphorus and K concentration (both measured
393 in 2010 only) of larch leaves increased considerably under fertilization, leading to
394 lower foliar N:P ($df = 40$, $t = -2.0$, $P = 0.048$) and N:K ratios ($df = 40$, $t = -2.4$, $P =$
395 0.024), while no change in nutrient ratios was found for pine leaves (Fig. 2).

396

397 The foliar N concentration of dwarf shrubs was independent of elevation (Table S2)
398 but increased with the fertilizer dose by up to 6–8 % in the NPK30 treatment in 2010
399 (df = 38, $t = 4.1$, $P < 0.001$, Fig. 2). While *V. gaultherioides* had, on average, higher
400 foliar N concentrations than *V. myrtillus* (df = 58, $t = 12.0$, $P < 0.001$), the response to
401 fertilization did not differ between these species. Dwarf shrubs had 17 [11, 22] %
402 higher foliar N concentrations when growing with larch instead of with pine (Fig. 2;
403 df = 20, $t = 5.9$, $P < 0.001$). As observed for larch trees, the N:P mass ratios of the
404 dwarf shrubs decreased significantly with increasing fertilization dose, but only in
405 plots with pine (Fig. 2; df = 38, $t = -2.5$, $P = 0.016$) and not under larch. Similarly,
406 foliar N:K ratios of dwarf shrubs decreased in fertilized plots with pine only (Fig. 2;
407 df = 38, $t = -3.9$, $P < 0.001$). N:Mg ratios remained unaffected by the treatment for all
408 species. These patterns for foliar N concentration were confirmed by the second
409 analysis using leaves harvested in 2016 (Fig. S4).

410

411 Foliar $\delta^{15}\text{N}$ in 2010 was unaffected by elevation, except for a slight increase at higher
412 elevations for pine (Table S2), but increased significantly with fertilization for both
413 tree species (Fig. 2, df = 40, $t = 5.9$, $P < 0.001$). This increase was much stronger for
414 pine than for larch (df = 40, $t = 3.0$, $P < 0.01$), and larch leaves were significantly less
415 depleted in ^{15}N than pine leaves (df = 20, $t = -4.9$, $P < 0.001$). Foliar $\delta^{15}\text{N}$ of dwarf
416 shrubs was also unaffected by elevation and $\delta^{15}\text{N}$ values increased with fertilization
417 (Fig. 2, df = 38, $t = 6.0$, $P < 0.001$). The response was similar between species for
418 dwarf shrubs and independent of the tree species growing in the plot. The second
419 analysis in 2016 confirmed the $\delta^{15}\text{N}$ signals observed in 2010 (Fig. S4).



421

422 **Figure 2** Effects of NPK fertilization, corresponding to 15 (NPK15) or 30 kg N ha⁻¹ a⁻¹ (NPK30), on N
 423 concentrations, mass ratios of N:P and N:K, and $\delta^{15}\text{N}$ values in leaves of *Larix decidua* (*Ld*), *Pinus*
 424 *uncinata* (*Pu*), *Vaccinium myrtillus* (*Vm*) and *Vaccinium gaultherioides* (*Vg*) in 2010. Means and 95%
 425 confidence intervals are shown. Point estimates and regression lines were modelled separately by
 426 treating the fertilizer dose as either a categorical or a numeric variable.

427

428 GROWTH OF TREE SPECIES

429 Before the first fertilizer application in 2004, there was no difference between plots
 430 assigned to the different treatments in any of the tree growth traits (top- and side-
 431 shoot increment, ring width; $P > 0.2$ in each case). In 2016, the average ring width of
 432 larch trees growing in control plots was 1.7 [1.4, 2.1] mm at the lowest elevation and
 433 decreased to 1.3 [1.0, 1.5] mm at the highest elevation ($df = 106$, $t = -2.2$, $P = 0.028$).

434 Higher elevation was also associated with smaller tree diameter and tree height in
435 larch (Table S3), with a decrease in diameter from 11.0 [8.7, 13.3] cm at the lowest
436 elevation to 8.0 [6.2, 9.9] cm at the highest elevation ($df = 97$, $t = -1.8$, $P = 0.071$).
437 Larch height was 536 [452, 627] cm at the lowest and decreased to 374 [317, 437] cm
438 at the highest elevation ($df = 97$, $t = -2.8$, $P = 0.007$). Elevation did not affect
439 individual annual top- and side-shoot increments of either tree species (Table S4), and
440 it had no influence on tree height (166 [90, 266] at lowest vs. 139 [82, 211] at highest
441 elevation) or diameter (4.9 [1.3, 8.4] vs. 6.0 [2.8, 9.1]) of pine.

442

443 In larch, nutrient addition stimulated all three annually measured growth traits (top-
444 and side-shoot increment, ring width). The average effect across years varied from
445 13% to 20% in the NPK15 treatment and from 11% to 14% in the NPK30 treatment,
446 depending on trait (Table 1). The differences between the two fertilizer doses were
447 not statistically significant for any of the growth traits for larch ($P > 0.14$ for each
448 trait). Interannual differences in the response were statistically significant for side-
449 shoot increment only (Table S4), where stimulation mainly occurred in the second
450 half of the study period (2011–2016, Fig. 3). Fertilization led to a significantly larger
451 tree diameter, but not height, for larch (Table 1).

452

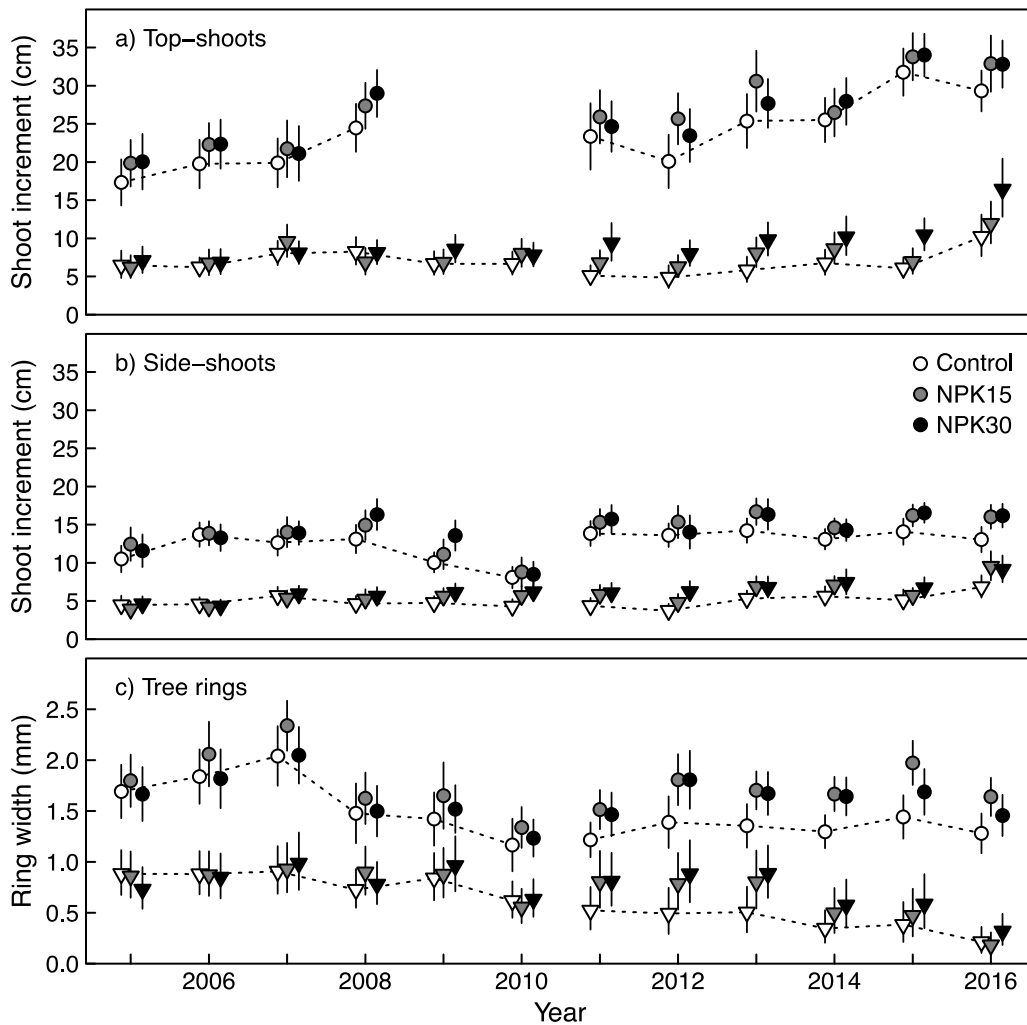
453 For pine, the response to fertilization varied significantly among years for each trait
454 (Table S4) and showed an initial phase with low fertilization effects followed by
455 stimulation in the second half of the study period (Fig. 3). The average stimulation
456 across years was significant for top- and side-shoot increment, ranging from 15 to
457 36% (Table 1), and marginally significant for ring width (+26% in the NPK30

458 treatment only). Top-shoot increment of pine responded significantly more to the
459 NPK30 than to the NPK15 treatment (Table 1, $df = 20$, $t = 2.96$, $P < 0.01$). Side-shoot
460 increments were also somewhat greater in the NPK30 than in the NPK15 treatment,
461 but the difference between the two fertilizer doses was not significant in this case.
462 Almost all pine trees from the lowest three sites, spanning 40 m of the total 140 m of
463 elevation investigated, died between 2005 and 2015. Fertilization had no effect on
464 tree survival in either species (controls were similarly affected).

465

466 Elevation had no statistically significant influence on the tree growth response to
467 fertilization, except for the side-shoot increment of pine in the NPK15 treatment
468 (Table S4), where fertilizer stimulation decreased with increasing elevation ($df = 91$, t
469 $= -2.4$, $P = 0.02$). However, this finding was not supported by data from the NPK30
470 treatment.

471



472

473 **Figure 3** Annual growth of top-shoots, side-shoots and tree ring width in larch (*Larix*
 474 *decidua*, dots) and mountain pine (*Pinus uncinata*, triangles) growing in control and
 475 fertilized plots, corresponding to 15 (NPK15) or 30 kg N ha⁻¹ a⁻¹ (NPK30). Means and
 476 95% confidence intervals are shown. Dotted lines connecting control values illustrate
 477 that the same individuals were measured in these years and apply to all treatments
 478 (not only control plots). Fertilizer was first applied in September 2004.

479

480 **Table 1** Model estimates for annual growth averaged across elevation and over all treatment years
 481 (2016 only for tree height and diameter). T-tests were used to determine the statistical significance of
 482 the differences between fertilized and control plots. Degrees of freedom were 20 for *L. decidua* (*Ld*)

483 and *P. uncinata* (*Pu*) and 37 for *V. myrtillus* (*Vm*) and *V. gaultherioides* (*Vg*). Bold numbers highlight
 484 significant ($P < 0.05$) and marginally significant ($P < 0.1$) differences.

Species	Measure	Control		NPK15				NPK30			
		Mean	95% CI	Mean	95% CI	<i>t</i>	<i>P</i>	Mean	95% CI	<i>t</i>	<i>P</i>
<i>Ld</i>	Tree ring (mm)	1.47	1.30, 1.63	1.76	1.60, 1.92	3.3	< 0.01	1.63	1.46, 1.79	1.8	0.09
	Top-shoot (cm)	23.6	21.4, 26.0	26.7	24.3, 29.0	2.5	0.02	26.3	24.0, 28.6	2.3	0.03
	Side-shoot (cm)	12.5	11.4, 13.6	14.1	13.0, 15.2	2.6	0.02	14.2	13.1, 15.3	2.7	0.01
	Height 2016 (cm)	443	404, 484	468	428, 510	1.4	0.16	470	430, 512	1.5	0.13
	Diam 2016 (cm)	9.4	8.2, 10.5	11.1	9.9, 12.3	3.7	< 0.01	10.3	9.1, 11.5	2.0	0.05
<i>Pu</i>	Tree ring (mm)	0.58	0.44, 0.76	0.69	0.52, 0.88	1.3	0.20	0.73	0.56, 0.93	1.9	0.07
	Top-shoot (cm)	6.7	5.7, 7.7	7.7	6.6, 8.8	2.2	0.04	9.1	7.9, 10.3	5.1	< 0.01
	Side-shoot (cm)	4.9	4.2, 5.7	5.7	4.9, 6.6	2.8	0.01	6.2	5.4, 7.1	4.3	< 0.01
	Height 2016 (cm)	151	124, 180	147	121, 177	-0.3	0.79	173	143, 205	1.6	0.11
	Diam 2016 (cm)	5.5	4.2, 6.8	5.7	4.4, 6.9	0.4	0.73	6.3	4.9, 7.6	1.4	0.17
<i>Vm</i>	Shoot (cm)	3.7	3.5, 3.7	4.0	3.8, 4.2	2.7	0.01	4.0	3.8, 4.2	2.8	< 0.01
<i>Vg</i>	Shoot (cm)	3.2	2.9, 3.5	3.5	3.1, 3.8	1.4	0.18	3.7	3.4, 4.1	2.7	0.01

485

486

487 GROWTH OF DWARF SHRUB SPECIES

488 As with trees, shoot increments of shrubs did not differ between treatments in 2004

489 before the fertilizer was applied ($P > 0.5$). In control plots, the mean annual shoot

490 increment was 3.7 cm for *V. myrtillus* and 3.2 cm for *V. gaultherioides*, independent

491 of elevation (Table 1). The response to fertilizer addition varied among years (Fig. 4).

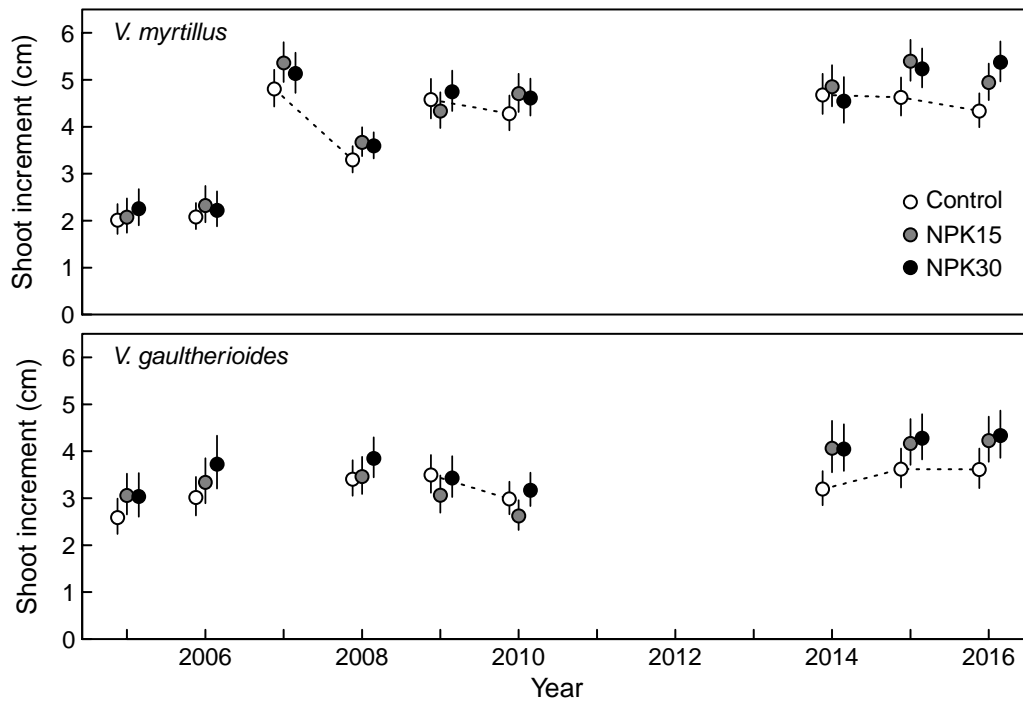
492 On average, both fertilizer doses stimulated the annual shoot increment of *V. myrtillus*

493 by ca. 8%, while *V. gaultherioides* responded to the NPK30 treatment only (16%

494 longer shoot increment, Table 1). The response to fertilization did not depend on

495 elevation or the tree species growing in the plot (Table S5).

496



497

498 **Figure 4** Annual shoot increment of *Vaccinium myrtillus* and *Vaccinium*
 499 *gaultherioides* growing in control or fertilized plots, corresponding to 15 (NPK15) or
 500 30 kg N ha⁻¹ a⁻¹ (NPK30). Means and 95% confidence intervals are shown. Dotted
 501 lines connecting control values indicate that the same individuals were measured in
 502 these years and apply to all treatments (not only control plots). Fertilizer was first
 503 applied in September 2004.

504

505 CLIMATIC EFFECTS ON THE FERTILIZER-RESPONSE

506 Summer (June, July and August) mean air temperatures were between 8.7 and 12.9 °C
 507 and did not significantly alter the response to fertilization, although the measured
 508 traits of trees and shrubs (except top- and side-shoot increment in pine) showed
 509 significantly increased growth in warmer years (Table S6). Our experiment covered
 510 0–4 frost events per season. Trees and shrubs showed reduced growth in years with
 511 more frequent frost events, except for top- and side-shoot increment in larch, which

512 were not significantly affected. The growth stimulation by fertilizer addition in tree
513 ring width of larch was significantly smaller in years with more frequent frost events
514 ($P = 0.012$, Table S6).

515

516 **Discussion**

517 Fertilizer addition to this high elevation treeline ecosystem for more than a decade
518 stimulated growth in all four investigated tree and dwarf shrub species. Even the
519 lower NPK-fertilizer dose with $15 \text{ kg N ha}^{-1} \text{ a}^{-1}$ was enough to stimulate growth in the
520 two tree species and in *V. myrtillus*. These findings strongly suggest that small
521 increases in soil nutrient availability may suffice to stimulate growth in this treeline
522 ecotone. In contrast to our hypothesis, the nutrient addition effect in larch did not
523 change with higher elevation in this ecotone, despite an almost halving of the height
524 and reduced annual radial growth in this species.

525

526 **LOW DOSE FERTILIZATION ENHANCES PLANT GROWTH**

527 While previous experiments with trees applied $85\text{--}175 \text{ kg N ha}^{-1} \text{ a}^{-1}$, leading to a
528 doubling or tripling of biomass production (Sveinbjörnsson 1992; Susiluoto et al.
529 2010), even our low dose treatment clearly enhanced growth. In cold regions, N
530 availability is often low in absolute terms, but related to productivity (and the short
531 growing season) the trends are not so obvious (Tranquillini 1979, Körner 2012)
532 because the nutrient cycle is tuned with the carbon cycle. Higher concentrations of N,
533 P and K in leaves, increased soil extractable N and higher $\delta^{15}\text{N}$ values in foliage
534 indicate that the mineral fertilizer indeed increased nutrient availability for plants,
535 even though a recent ^{15}N tracer study at this site showed that about 60% of N added as

536 NH_4^+ or glycine is rapidly immobilized in the soil (Dawes et al. 2017a), as is typical
537 for high elevation ecosystems on acidic soils (Gerzabek et al. 2004). The increase in
538 plant nutrient concentration by our comparably low fertilizer dose was similar to that
539 in the Scandinavian treeline study with birch using a much higher dose of NPK-
540 fertilizer (Sveinbjörnsson 1992), but we do not know whether birch would have
541 responded similarly to such low nutrient additions. We attribute the high
542 responsiveness of the treeline ecosystem in our study to low rates of nutrient addition
543 to a so far unexplored non-linearity of nutrient-growth relationships. Remarkably,
544 little additional growth stimulation was observed with the higher ($30 \text{ kg ha}^{-1} \text{ a}^{-1}$)
545 fertilizer dose compared with the lower dose. Our site has acidic soils covered with 5–
546 20 cm thick organic layers and intrinsically low rates of nutrient cycling compared to
547 forest soils in the temperate zone (e.g. Bednorz et al. 2000; Blaser et al. 2005;
548 Hagedorn et al. 2010). Accordingly, the lack of a surplus stimulation by the higher
549 fertilizer dose may indicate a low overall nutrient demand of growth, e.g. due to an
550 inherently low growth rate or because of thermal constraints on meristematic activity
551 (Hoch 2013). The 8–16% increase in dwarf shrub growth is low compared with
552 results from an alpine grassland at 2500 m a.s.l., where a doubling in biomass was
553 reported in response to $40 \text{ kg N ha}^{-1} \text{ a}^{-1}$ (Schäppi & Körner 1996).

554

555 *SPECIES-SPECIFIC GROWTH RESPONSES*

556 Trees and dwarf shrubs showed a similar stimulation by nutrient addition in contrast
557 to our expectations that dwarf shrubs would be more responsive than trees because of
558 a more favourable microclimate. This result may be related to spatial and temporal
559 temperature variation. First, the microclimate in the understory vegetation does not

560 warm up as much as it does in open terrain (Körner 2012). Thus, trees and dwarf
561 shrubs experienced similar soil temperatures, at least in the rooting zone. Second, the
562 ongoing climatic warming by 2 K (Rixen et al. 2012) during the last four decades has
563 probably already relieved trees from thermal constraints of growth to some extent.

564

565 Although there was a similar fertilization effect on both growth forms, there was a
566 difference in the response between the two dwarf shrubs. While shoot increment
567 length of *V. gaultherioides* was stimulated by the higher fertilizer dose only,
568 responses of *V. myrtillus* saturated at the lower fertilizer dose (no difference between
569 the two doses). In a separate experiment within the same afforestation used in our
570 study, Dawes et al. (2011) found that growth of *V. myrtillus* responded more than that
571 of *V. gaultherioides* to six years of experimental soil warming by 4 K, a treatment that
572 led to enhanced nitrogen availability (Dawes et al. 2017b). *Vaccinium myrtillus* has a
573 wider elevational distribution range than *V. gaultherioides* (Lauber et al. 2012) and
574 might have a competitive advantage under changing growth conditions. However, it
575 was also found to be more prone to freezing damage when growing in warmer soils
576 (Martin et al. 2010), which could ultimately have a larger impact than growth
577 stimulation by warming or increased nutrient availability. It had been shown, although
578 with higher addition rates of N (>100 kg ha⁻¹), that fertilization delays bud formation
579 in autumn, and thus winter dormancy and freezing tolerance, in *V. myrtillus* (Körner
580 1984).

581

582 Positive effects of fertilization on the rate of tissue formation are commonly observed,
583 but may be counteracted by increased pathogen impact (Herms & Mattson 1992,

584 Rühmann et al. 2002, Blodgett et al. 2005) or reduced freezing tolerance (Hellergrén
585 1981). In addition, faster growth from additional N may result in lower tissue
586 concentrations of lignin (Pitre et al. 2007, Li et al. 2012), which in turn could increase
587 the susceptibility to mechanical damage from snow breakage, wind, rock fall or
588 avalanches and ultimately lead to biomass loss. There is also evidence that fertilizer
589 addition can reduce the success of afforestation with small saplings, largely due to
590 fungal diseases—work that actually had been conducted at our study site (Keller
591 1970). We found that frequent frost events reduce, but not reverse, the growth
592 stimulation in larch. Nevertheless, stimulated growth and unchanged mortality in
593 response to twelve years of moderate nutrient addition in the current experiment
594 suggests that the adult trees examined here were not negatively affected by the
595 fertilizer treatment. Negative consequences of improved nutrition, and thus vigor,
596 could be associated with stochastic phenomena such as heavy snow pack (mechanical
597 damage), certain snow melt regimes (fungal pathogens) or epidemic insect outbreaks
598 (e.g. larch budmoth), and may take more time to materialize.

599

600 GROWING SEASON TEMPERATURE DID NOT MODULATE THE 601 FERTILIZER RESPONSE

602 Despite the positive association between summer temperature and annual growth, the
603 interannual variation of the fertilizer response was unrelated to interannual
604 temperature variation among growing seasons in trees and shrubs. To some extent,
605 these results may be confounded by an accumulation of added nutrients in the plant-
606 soil-microbe system over the study duration. However, we expect this effect to be
607 small, as trees and shrubs generally did not respond to a surplus of nutrients (the

608 higher fertilizer dose) and longer term ¹⁵N studies in forest soils reveal added N to be
609 rapidly bound to stable soil organic matter pools (Hagedorn et al., 2005; Schleppei et
610 al. 2017). The lack of interaction between summer temperature and fertilizer is in line
611 with the absence of such an interactive effect across elevation within the ecotone. The
612 overall lack of fertilizer-temperature interaction is in contrast to the mountain birch
613 data that revealed the greatest responsiveness to nutrient addition at the highest
614 (coldest) of three sites spanning roughly 200 m in elevation (Sveinbjörnsson et al.
615 1992). These differences may reflect site-specific effects, differences between
616 evergreen and deciduous species, or the different experimental durations and rates of
617 fertilizer addition.

618

619 Within the treeline ecotone covered in this study, growth of pine and larch decreased
620 considerably with increasing elevation during the 30 years before our experiment
621 started (Barbeito et al. 2012). This is typical for high elevation treelines, where the
622 distance between closed montane forest and the krummholz belt is often not more
623 than 50–100 m in elevation (Körner 2012). The elevation-associated decline in larch
624 ring width observed in our study indicates that temperature is still a major growth-
625 limiting factor for this species within the afforestation site. Notably, apical and lateral
626 increments in shoots showed no significant elevation-associated patterns, but these
627 traits may not reflect the overall crown increment, which depends on the number of
628 shoots per crown surface area, branching patterns, and annual shoot wasting. Thus,
629 apical and lateral increments of single shoots may overestimate growth of larch at
630 higher elevation, where trees were clearly much smaller. The lack of an elevation-
631 associated decline of growth in pine during the study period may relate to the
632 generally low vigor and often crippled shape of these trees at the site. While Barbeito

633 et al. (2012) found decreasing growth of pine with increasing elevation within the
634 afforestation during the three decades before our experiment, the effect diminished
635 over time and was comparably weak in the most recent decade before our experiment
636 started (1995 to 2005).

637

638 A recent decrease of dwarf shrub cover at the lowest locations, presumably coupled
639 to an increase in visibly more vigorous (and therefore nutrient-demanding) understory
640 species, could be another explanation (see Fig. S5). The growing season temperature
641 increased by ca. 2 K in the region since the afforestation site was established in 1975
642 (Rixen et al. 2012). This warming (corresponding to 300 to 400 m of elevation) may
643 have masked the smaller spatial and year-to-year variation in temperature. In a study
644 close to our site, similar seedling survival at low and high elevations suggested that
645 the current treeline position lags behind climatic changes (Zurbriggen et al. 2013).
646 This indicates that temperature limitation of growth has been reduced over the past
647 few decades, as was also observed for other treelines in the Swiss Alps (Jochner et al.
648 2018).

649

650 For seedlings of the same tree species as investigated in this study, it was shown that
651 fertilizer responses were diminished at critically low mean temperatures of around 6
652 °C in a growth chamber, but that warmer air or soil temperature (12 °C) enabled
653 positive growth responses to fertilization (Hoch 2013). Similarly, Iivonen et al. (1999)
654 found that 1-year-old *Pinus sylvestris* seedlings grown at different root zone
655 temperatures showed growth stimulation by fertilization only above 13 °C. Hoch
656 (2013) argued that growth stimulation by nutrient addition may occur only above such

657 critically low temperatures. Our data suggest that even the uppermost trees grew far
658 from a thermal limit of growth.

659

660 FERTILIZATION ALTERS NUTRIENT BALANCES

661 While primary production of most terrestrial ecosystems on a global scale is
662 considered to be N limited (Vitousek & Howarth, 1991), we found lower foliar N:P
663 ratios with fertilization in three out of four species, suggesting that growth is limited
664 more by P than N (Güsewell 2004). The only previous study in which trees at treeline
665 received N and P additions separately was that with mountain birch, where no
666 indication of P limitation was observed while N addition clearly stimulated growth
667 (Sveinbjörnsson 1992). Perhaps continuous atmospheric N deposition during the last
668 century has decreased the capacity for further growth stimulation by N addition at our
669 site. Alternatively, lower N:P ratios may be related to a greater retention of N than of
670 P in the soil due to microbial immobilization, a lack of P sorption in the thick organic
671 layers, or a higher supply of P compared to N, a likely scenario when considering that
672 our fertilizer had an N:P ratio of five while the foliar N:P ratios of the investigated
673 plants were about twice as high. Altered mechanisms of nutrient uptake are supported
674 by higher $\delta^{15}\text{N}$ values in all plant species already at low levels of fertilization
675 (corresponding to $15 \text{ kg N ha}^{-1} \text{ a}^{-1}$). This finding indicates either that the plants took
676 up more N from the supplied NH_4^+ (Garten 1993, Craine et al. 2009, Miller &
677 Bowman 2002) or that there was a decrease in the proportion of organic N acquired
678 by plants through mycorrhizal association (Emmerton et al. 2001, Hobbie & Colpaert
679 2002). Mycorrhizal activity has frequently been observed to decline with N
680 fertilization (Wallander & Nylund 1992; Nilsson & Wallander 2003; Högberg et al.

681 2010). Further, in an experiment near our study site where soil warming led to greater
682 N availability, Solly et al. (2017b) observed a shift in the fungal community
683 composition towards more nitrophilic species.

684

685 *[Conclusions]*

686 Our findings demonstrate that even a relatively low dose of fertilizer can enhance
687 growth of woody species near the treeline, confirming the sensitivity of low
688 temperature ecosystems to changes in nutrient availability in the soil. Hence, despite a
689 limitation of plant growth by low temperatures at high elevation, even a small
690 improvement of nutrient supply, for instance by increased atmospheric deposition or
691 enhanced nutrient mineralization in warmer soils, can cause changes in high elevation
692 treeline ecosystems. Our experimental site and all 'natural' treelines in the region
693 experienced a 2 K warming over the past four decades, which has reduced thermal
694 limitation of growth (Jochner et al. 2018) and may have masked interactions between
695 fertilizer addition and more subtle year-to-year or spatial temperature differences.
696 Thus, while treeline trees and associated dwarf shrubs benefit from nutrient addition
697 in terms of growth, our study does not allow to answer whether nutrient availability
698 influences the position of treelines. A central remaining question is whether greater
699 tree vigor and/or higher tissue nutrient concentrations exert negative long-term fitness
700 effects in such marginal habitats. Implications of faster growth for the long-term
701 fitness of treeline species await additional research focusing on reproduction, life-
702 span (mortality) and stress tolerance. Nevertheless, faster growth rates with increased
703 nutrient availability may speed up the anticipated upward shift of treeline ecotones as
704 a consequence of climate warming.

705

706 **Acknowledgements**

707 The authors thank S. Stolz, A. Nussbaumer, K. Birmann, S. Mannes, M. Pattaroni, N.
708 Hardegger and T. Schmid for assistance with field work. We also thank two
709 anonymous reviewers for their critical comments on the manuscript.

710

711 **Authors' contributions**

712 CR designed the study in consultation with PB, CK and SW. PM, MM, DV, and FH
713 collected data, and PM, MM and MD completed the data analysis. PM led the writing
714 with revisions and contributions from all authors. All authors approved the final
715 version.

716

717 **Data accessibility**

718 The data used in this study will be available at figshare.com.

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