



1 Article

2 **Permafrost regime affects the nutritional status and**  
3 **productivity of larches in Central Siberia**4  
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17 \* Correspondence: prokushkin@ksc.krasn.ru; Tel.: +79131782531718 **Abstract:** Permafrost exerts strong controls on forest development through nutrient availability.  
19 The key questions of this study addressed the effect of site conditions on mass-based macroelement  
20 concentration and stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) dynamics during the growing season, and nutrient  
21 stoichiometry and resorption efficiency in foliage of two common larch species in Siberia. Foliar  
22 nutrient (N, P and K) concentrations of larches grown on permafrost soils were exceptionally high  
23 in juvenile needles as compared to those from a permafrost-free region, but were 2-fold lower with  
24 needle maturation. Within permafrost terrain trees from sites with a warmer and deeper soil active  
25 layer had 15-60% greater nutrient concentrations and higher  $\delta^{15}\text{N}$  in their needles compared to  
26 shallower, colder soils. Larch of permafrost-free sites demonstrated enrichment of foliage in  $^{15}\text{N}$   
27 (+1.4 to +2.4 ‰) in comparison to permafrost terrain (-2.0 to -6.9 ‰). Seasonal dynamics of foliar  
28  $\delta^{13}\text{C}$  tended to decrease from June to August at all sites, positively correlating with mass-based N  
29 concentrations ( $r=0.69$ ,  $p<0.05$ ) and negatively with C:N ratio ( $r=-0.79$ ,  $p<0.05$ ). With senescence,  
30 nutrient concentrations in larch needles decreased significantly by 60-90%. This strong ability of  
31 larch to retain nutrients through resorption is the essential mechanism that maintains tree growth  
32 early in the growing season when soil remains frozen. High resorptive efficiency found for K and P  
33 for larches established on permafrost suggests nutrient limitation of tree growth within the Central  
34 Siberian Plateau not only by N, as previously reported, but also by P and K. Along with increased  
35 biomass (up to 50-fold), higher nutrient concentrations and  $^{15}\text{N}$  enrichment of foliage in warmer  
36 sites indicate a strong response of larch stand productivity to a deepening of the soil active layer.37 **Keywords:** permafrost, Siberian *Larix* spp., foliar nutrients, foliar  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , spatio-temporal  
38 variation, stoichiometry, nutrient resorption  
3940 **1. Introduction**41 Absorption and storage of large amounts of atmospheric carbon (C) in the forest biomass and  
42 soil of the Northern hemisphere are among the central issues of the global greenhouse gas balance  
43 [1]. In this context, vast larch forests across Siberia may play an important role for carbon  
44 sequestration given the unique characteristics of *Larix* spp. [2] including its broad geographic  
45 distribution [3,4], the high photosynthetic capacity [5-7] and tendency to reach high stand biomass

46 under favourable conditions [2,8]. Mature larch stands across Siberia function nowadays as a  
47 relatively weak to medium sink of atmospheric CO<sub>2</sub> [9-11], and temperature, water and nutrient  
48 supply are known to be the most important abiotic variables controlling the sink strength under  
49 current conditions.

50 Although *Larix* species in continental Siberia are generally exposed to a water deficit [6,7,10], to  
51 offset the short growing period they typically show the highest photoassimilation rates among  
52 coniferous tree species when climatic conditions are favorable, not only on a yearly basis but also on  
53 a daily basis [6]. Such a strategy, nevertheless, is associated with greater water conductance, much  
54 higher transpiration water losses [6] and lower water use efficiency (WUE) for assimilated carbon  
55 [5]. This low WUE is particularly evident in the low values of  $\delta^{13}\text{C}$  of foliage in comparison to  
56 co-occurring evergreen conifers [2,5]. There was a high spatial variability of larch foliar  $\delta^{13}\text{C}$  among  
57 20 locations in Northern hemisphere [5], as well as significant seasonal changes of foliar  $^{13}\text{C}$  within a  
58 single site [9], indicating that environmental controls of larch foliar  $\delta^{13}\text{C}$  and thus WUE still remain  
59 uncertain.

60 In conjunction with high photosynthetic rates, larch species of Northern hemisphere are  
61 characterized by the highest concentrations of nitrogen [2,5,9,12] and other macronutrients (e.g. P  
62 and K)[12] in foliage relative to evergreen conifers, very likely due to annually renewed needles.  
63 Thus, high nutrient demand to build foliar biomass may constrain the ability of larch taiga on  
64 permafrost soils to act as a sink of atmospheric C [13,14]. Globally, N and P are the most common  
65 nutrients limiting plant productivity and atmospheric C sequestration rates throughout terrestrial  
66 biomes [15-18]. In particular, N limitation is shown to be strongest in deciduous needle-leaf forests  
67 in high-latitude regions of the Northern Hemisphere due to slow N mineralization rates [13,18].  
68 Nitrogen concentrations and natural isotopic abundance of N ( $\delta^{15}\text{N}:\text{N}^{14}$ ) in plant foliage integrate  
69 ecosystem biogeochemical processes involved in N cycling and its sources within an ecosystem  
70 [19,20]. In particular, foliar  $\delta^{15}\text{N}$  in boreal forest ecosystems is reported to respond positively to an  
71 overall increase of N availability in soils, as larger soil N "stimulates" loss of depleted N in soluble  
72 and gaseous forms and results in the  $\delta^{15}\text{N}$  enrichment of the remaining pool. An important  
73 mechanism to offset nutrient limitation in plants in boreal biome is their symbiosis with fungi that is  
74 significantly changing the isotopic composition of N in host plant in comparison to bulk N source in  
75 soils [20]. *Larix* species are reported to rely on ectomycorrhizal fungi [21] that are responsible for the  
76 most significant N depletion of host plant tissues [22]. All these factors might be of particular  
77 importance for permafrost terrains, where seasonal thawing of soil causes a gradual increase of soil  
78 depth (soil active layer) that is accessible for root exploration (e.g. decreasing dependence on fungal  
79 N) and, respectively, an uptake of isotopically distinct N early and late in the growing season (i.e.  
80 light N in topsoil vs. heavy N in subsoil) [23].

81 The resorption (retranslocation) of nutrients prior to leaf senescence is the main mechanism of  
82 nutrient preservation at the annual time scale [2,24-26], thus influencing whole tree survival on  
83 permafrost [27]. Indeed, nutrient retranslocation may supply a considerable part of the tree's  
84 nutrient requirements for new biomass production in the beginning of next growing season, when  
85 the soil remains frozen. N- and P-resorption efficiency, which is defined as the proportion of  
86 maximum nutrient pool resorbed prior to leaf abscission, ranges from 0 to 80% according to species  
87 and environmental conditions [25,26,28,] and is generally higher for *Larix* spp. in comparison to  
88 sympatric evergreen conifers and deciduous broadleaved [2].

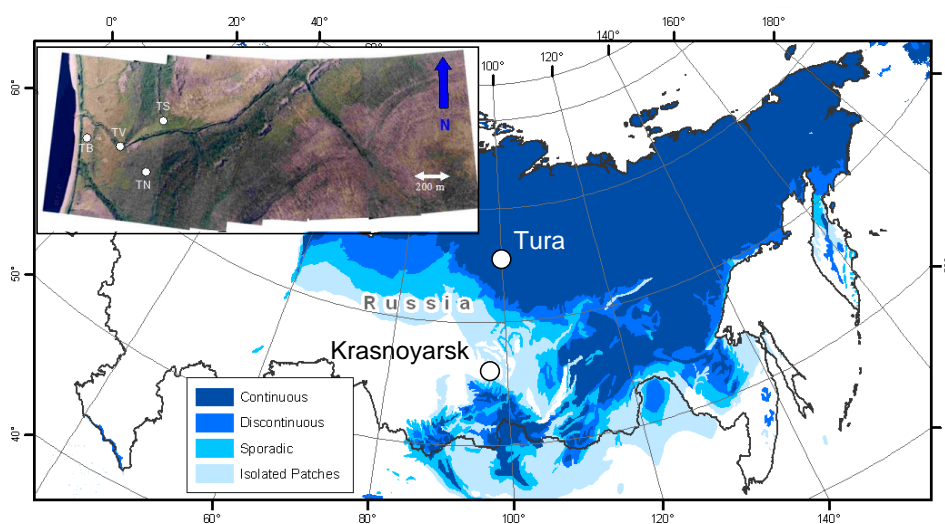
89 Within permafrost-affected landscapes hydrology, thermal properties and biogeochemical  
90 processes of an ecosystem may strongly vary among specific sites. Sites with northern aspects  
91 receive lower insolation than those with southern aspects, resulting in cooler soils, slower thawing  
92 rates, and a shallower active layer. Poorly-drained habitats in depressions facilitate the development  
93 of forested peat bogs, which hampers mineralization of plant residues and in turn, induces lower  
94 soil temperatures due to higher soil insulation [29]. As a consequence, forest peatlands are nutrient  
95 poor as they primarily rely on atmospheric input of nutrients. Therefore, specific sites within the  
96 permafrost terrain may serve as a natural laboratory for analysing various aspects of nutrient cycling  
97 in forest ecosystems developed on cryosols.

98 The aim of this study was to estimate the effects of permafrost on the nutritional status of larch  
 99 trees in Central Siberia and to assess possible responses of larch stands to projected warming at high  
 100 latitudes. Our approach was to make use of a natural experimental set-up provided by the strong  
 101 micrometeorological differences among sites within permafrost terrain: (i) Northern slopes with  
 102 continuous permafrost zone; (ii) adjacent south-facing stands with deeper active layer, (iii) a fertile  
 103 soil in the valley and (iv) a forested peatland and compared it with permafrost free sites further  
 104 south. At these sites, we analysed the seasonal evolution of foliar concentrations of C, N, P, K and  
 105 the and stable C and N isotope composition ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of the main larch species (*Larix gmelinii*  
 106 [Rupr.] Rupr and and *Larix sibirica* Ledeb). In our study, we address the following questions: 1) what  
 107 are the temporal changes in foliar nutrient concentrations, stable isotope composition and nutrient  
 108 stoichiometry throughout the growing season on permafrost and permafrost-free soils? 2) What are  
 109 the primary nutrient limitations for *Larix* productivity at the leaf and stand scale across a gradient of  
 110 permafrost regime and how does *Larix* cope with a low nutrient supply? 3) How do permafrost and  
 111 its degradation likely affect nutrient availability and productivity of Siberian larch forests?

## 112 2. Materials and Methods

### 113 2.1. Study sites

114 Foliar nutrients of *Larix* spp. have been sampled in two regions of Central Siberia which differ  
 115 in the extent of permafrost: the Tura site within the zone of continuous permafrost, and the  
 116 Krasnoyarsk site in a permafrost-free area (Figure 1). Four tree stands of Gmelin's larch (*Larix*  
 117 *gmelinii* [Rupr.] Rupr) were chosen near the Tura settlement in Central Siberia (64°19' N, 100°15' E) to  
 118 represent different sites: south-facing slope, north-facing slope, *Sphagnum* peatbog and stream valley  
 119 (hereafter referred to as TS, TN, TB and TV, respectively) (Figure 1, insert). A detailed description of  
 120 the plots was provided by Viers et al. [30] and given in Tables 1 and 2. Larch stands of all plots are  
 121 developed on soils that originated from basalt parent rock, but range drastically in active layer  
 122 thickness (Table 2). Importantly, three stands (TS, TN and TB) were regenerated after a ground fire  
 123 in 1899. As a result of similarities in parent rock and fire history, the stand net carbon assimilation  
 124 and nutrient cycling are thought to be controlled by intrinsic site-specific soil hydrothermal  
 125 conditions.



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127 **Figure 1.** The map of Russia representing permafrost distribution (adapted from Brown *et al.* 1998)  
 128 and location of study sites in Central Siberia. Inserted image shows location of plots in various  
 129 habitats within permafrost site (Tura): TN – north-facing slope, TS – south-facing slope, TV – stream  
 130 valley (riparian zone) and TB – *Sphagnum* peatbog.

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Table 1. Plot and tree stand characteristics of the study sites in Central Siberia.

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Stand dominant	Plot name	Latitude/longitude	Stand density, tree/ha	Age, yrs	Mean tree ring width, mm	DBH, cm	Tree height, m	Aboveground biomass, Mg/ha		
								trunk	needle	total
Krasnoyarsk: permafrost-free terrain										
<i>L. gmelinii</i>	L.g. KD	55°59'N 92°45'E	760	32	3.55±2.56	17.5	14.8	38.6	7.7	70.5
<i>L. sibirica</i>	L.s. KD	55°59'N 92°45'E	800	32	3.58±2.50	24.0	16.3	42.0	6.2	76.3
Tura: continuous permafrost terrain										
<i>L. gmelinii</i>	North-facing slope (TN)	64°19'21"N 100°14'53"E	4400	99	0.11±0.03	5.8	7.7	26.9	0.5	28.2
<i>L. gmelinii</i>	South-facing slope (TS)	64°19'32"N 100°15'32"E	2700	91	0.17±0.05	9.3	11.3	52.3	1.6	56.6
<i>L. gmelinii</i>	<i>Sphagnum</i> peatbog (TB)	64°19'30"N 100°15'53"E	2480	86	0.11±0.05	4.0	4.1	5.6	0.3	7.0
<i>L. gmelinii</i>	Riparian zone (TV)	64°19'29"N 100°15'07"E	1100	156	0.51±0.20	15.0	12.9	55.9	7.0	79.0

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**Table 2.** Soil characteristics of plots selected in permafrost terrain. Data presented as mean ( $\pm$ SD).185  
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Plot Soil type*	Organic layer				Mineral soil								rooting depth, cm		
	OC, kg/m <sup>2</sup>	$\delta^{13}\text{C}$ ‰	N, g/m <sup>2</sup>	$\delta^{15}\text{N}$ ‰	OC, kg/m <sup>2</sup>	$\delta^{13}\text{C}$ ‰	N, g/m <sup>2</sup>	$\delta^{15}\text{N}$ ‰	active layer thickness, cm <sup>^</sup>					T <sub>5 cm, &amp;</sub> oC	
									June	July	August	Sept			
Krasnoyarsk: permafrost-free terrain															
L.g. KD	0.4	-	16	-	2.9	-	251	-	-	-	-	-	-	9.2	70
L.s. KD	0.3	-	17	-	3.2	-	342	-	-	-	-	-	-	8.9	62
Tura: continuous permafrost terrain															
TN	2.1	-28.35	54	-0.20	6.6	-27.12	307	3.24	1±1	25±12	36±11	42	2.8	12	
TS	0.8	-29.04	22	-1.14	5.4	-27.47	309	3.43	18±8	86±15	112±26	123	6.6	64	
TB	6.4	-28.64	96	0.19	5.5	-28.02	425	1.58	0	1±2	15±8	20	0.1	0	
TV	1.8	-29.67	60	-0.06	7.3	-28.21	365	2.31	5±2	52±16	63±19	88	4.1	45	

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\*Keys to soil taxonomy (1998)

©Topsoil layer (0-10 cm)

^At the date of needle collection

&amp;Mean summer (June-August) soil temperature at 5 cm depth for two consecutive years (2005-2006)

236 The climate in Tura is cold and dry with a mean annual air temperature of  $-9.1^{\circ}\text{C}$  (1929-2012).  
237 Mean monthly air temperature varies from about  $-36^{\circ}\text{C}$  in January to  $16.5^{\circ}\text{C}$  in July. Annual  
238 precipitation in this region is 371 mm, with 60-70% occurring during summer.

239 For comparison, *L. gmelinii* and *L. sibirica* stands were selected in adjacent plantations in the  
240 arboretum of the V.N. Sukachev Institute of Forest near Krasnoyarsk (Forest-steppe ecotone)  
241 ( $55^{\circ}59'N$   $92^{\circ}45'E$ ). The mean annual air temperature in Krasnoyarsk is  $0.9^{\circ}\text{C}$  (1891-2009). Mean air  
242 temperature varies from about  $-16.8^{\circ}\text{C}$  in January to  $19.1^{\circ}\text{C}$  in July. Mean annual precipitation is 500  
243 mm (1967-2009). The soil is seasonally frozen (November-April). Ground vegetation is dominated by  
244 graminoids and a considerable portion of the area is covered with larch needle litter (for stand and  
245 soil characteristics, see Tables 1 and 2).

## 246 2.2. Sampling and analyses

### 247 2.2.1. Stand inventory and tree biomass measurements

248 In mid-August of 2006, we have established plots with 20 m long sides that served as the edge  
249 to define the start of a tree census. When counts within this 20 m border reached ca. 200 trees  
250 (adapted from the Russian standard for stand inventory), which also includes saplings ( $<1.3$  m  
251 height) and dead trees, plot length was measured and total area was calculated. Taking into account  
252 different densities of trees, plot area varied among sites from roughly 200 to 1800  $\text{m}^2$ . For every tree  
253 on the plot we have measured tree height, D0, DBH (the diameters at zero height and at breast  
254 height), crown length and assessed whether the tree was living or dead. Mean tree height and DBH  
255 were calculated for living trees in every stand. To estimate stand level total aboveground biomass  
256 and biomass of its fractions (trunk, branches and needles) we applied allometric equations based on  
257 model tree sampling. For this purpose, in every habitat from 7 to 10 trees from each diameter class  
258 (1-2 cm step) was logged and weighed for fresh biomass of trunk and crown (branches with needles)  
259 separately. Then subsamples of trunk (wood discs from D0, Ddbh,  $2/3$  and  $3/4$  height), thick ( $>2$  cm)  
260 and thin ( $<2$  cm) branches and needles from bottom, middle and top part of crown (3 mean  
261 branches) were sampled and dried in the oven at  $105^{\circ}\text{C}$  to obtain dry weight conversion coefficients  
262 for the respective fraction of aboveground biomass. Then plot-specific allometric equations were  
263 developed relating component biomass to diameter at breast height (DBH) and tree height ( $h$ ) ( $Y = \beta$   
264  $X\alpha$ , where  $Y$  – biomass,  $X$  – DBH or  $h$ ). The best fits for prediction of biomass were shown for  
265 diameter at breast height in all plots ( $R^2 > 0.93$  for total and trunk biomass,  $R^2 = 0.58-0.83$  for branches  
266 and needles). Further site- and fraction-specific allometric equations have been used for calculations  
267 of total aboveground biomass and fractions.

268 To obtain tree stand age and mean tree ring width (TRW), wood discs and cores of at least 20  
269 trees have been analyzed in the laboratory by dendochronological methods [31]. Fire year (1899) has  
270 also been estimated dendrochronologically by dating fire scars of discs from 2-5 trees that survived  
271 the fire at every habitat.

### 272 2.2.2. Soils

273 Organic and mineral soil samples have been collected along the 10 m transect at the centre of  
274 each plot. The soil active layer depth (ALD) (annually thawed depth to permafrost) and surficial  
275 organic layer column (moss-lichen stratum and organic soil layer) have been measured by steel rod  
276 every 1 m ( $n=11$ ). To measure stocks of organic layer we sampled 5 column replicates every 2 m.  
277 Collected material was separated into the live portion of ground vegetation and the organic soil  
278 layer (O). Subsamples of both portions were oven dried ( $105^{\circ}\text{C}$ ) to determine the ratio between  
279 moss-lichen stratum and organic soil layer, and bulk densities. Then the dependence between  
280 thickness and stock of organic layer column was used to calculate the mean transect-specific organic  
281 layer stock.

282 Sampling of mineral soil has been performed in soil pits beneath sampled organic layers ( $n=5$ )  
283 by  $100\text{ cm}^3$  cylinders with 3 replicates at every 10 cm depth for the entire active layer to permafrost  
284 table (20-120 cm). Rooting zone was determined as the maximum depth at which larch roots

285 appeared in soil pits. Under field conditions all fresh soils were sieved through a 2-mm mesh sieve  
286 with further removal of finer roots in the 2 mm fraction. In parallel, one cylinder sample has been  
287 collected to obtain soil bulk density by oven drying at 105°C in laboratory conditions. Then the 2 mm  
288 soil fraction and bulk organic layer samples were divided into subsamples which were used for C  
289 and N determination performed on finely ground samples (mixer mill, Retsch, Germany) and oven  
290 dried at 80°C (48 hours). Total mass-based concentrations of nitrogen and carbon were measured by  
291 Cu-O catalysed dry combustion at 900 °C with ≤0.5% precision for standard substances (Elementar  
292 Vario Maxi CHNS analyser, Elementar Analysensysteme GmbH, Hanau, Germany). Carbonate C  
293 was not detected in soils and all C in soils was recovered in organic form. The isotope ratios ( $\delta^{13}\text{C}$   
294 and  $\delta^{15}\text{N}$ ) were determined on soil samples (organic (O) layer and humic (A) horizons) collected in  
295 2011 in the same sites using a Delta-S isotope ratio mass spectrometer (Finnigan MAT, Bremen,  
296 Germany) linked to elemental analyzer (EA-1108 Carlo Erba, Italy) via a variable open split interface  
297 (ConFlo-II; Finnigan MAT, Bremen, Germany). The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were determined in continuous  
298 flow mode. This guarantees a high sample throughput rate with good precision for  $\delta^{13}\text{C}$  ( $r \pm 0.1\%$ )  
299 and  $\delta^{15}\text{N}$  ( $r \pm 0.2\%$ ). The isotopic values were expressed in the  $\delta$  notation relative to the international  
300 standards:

$$301 \quad \delta_{\text{sample}} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000;$$

302 where  $R_{\text{sample}}$  is the molar fraction of  $^{13}\text{C}/^{12}\text{C}$ , or  $^{15}\text{N}/^{14}\text{N}$  ratio of the sample and  $R_{\text{standard}}$  of the  
303 standards Vienna Pee Dee belemnite for C and atmospheric  $\text{N}_2$  for N.

304 Values of total C and N were normalized to absolute dry mass of soil (after drying at 105° C).  
305 Further, bulk density of soil and respective C and N mass-based concentrations were used to  
306 calculate their stocks in layers of organic and mineral soil, which in the latter case was limited to 0.5  
307 m for easier comparison among sites that varied greatly in active layer depth (20-120 cm).  
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### 309 2.2.3. Larch needles

310 Samples of larch needles were collected during the growing season of 2006, taking into account  
311 the differences in phenology between two sites located in northern and southern parts of the region,  
312 respectively. Sampling was carried out four times: started from juvenile needles on June 7 in Tura  
313 ( $60 \pm 4\%$  of maximum mass and  $73 \pm 6\%$  of length attained in July) and May 25 in Krasnoyarsk ( $66 \pm 5\%$   
314 of maximum mass and  $81 \pm 3\%$  of length attained in August); continued with mature needles (July 18  
315 and 21, respectively in Tura and Krasnoyarsk), then senescing needles (August 23 and 25) and ended  
316 at the coloured phase (yellow) just during needle shedding (September 12 and October 20). Samples  
317 of larch short shoot needles from 3-5 mid-crown branches were collected on every plot from three  
318 trees representing the mean tree of the stand (diameter at breast height and tree height) and similar  
319 live status (crown development).

320 After collection, the plant material was first cleaned on site with ultrapure water to remove  
321 surface particles, air dried and stored in clean plastic bags. Back in the laboratory, samples were  
322 dried at 80°C for 48 hours and finely ground using a mixer mill (Retsch, Germany). Total nitrogen  
323 and carbon mass-based concentrations and isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) in bulk samples of larch  
324 needles were measured by the same method as for the soil samples. As described earlier [30] for the  
325 analysis of phosphorus and potassium, samples were processed in a clean room (class A 10000).  
326 Between 100 and 200 mg of needle material was first digested in hydrogen peroxide ( $\text{H}_2\text{O}_2$ ) for 24  
327 hours at ambient temperature and further digested in  $\text{HNO}_3 + \text{HF}$ , for 36 hours at 80°C, then in HCl  
328 for 36 hours at 80°C, and finally, by HCl- $\text{HNO}_3$  treatment for 36 hours at 80°C. Measurements of P  
329 and K were conducted by ICP-MS (Agilent 7500 CE) using 3-point calibration against a standard  
330 solution of known concentration [30]. Indium and rhenium were used as internal standards to  
331 correct for instrumental drift and eventual matrix effects. The international geostandards Apple  
332 Leaves SRM 1515 (from NIST, USA), lichens BCR-CRM 482 (from BCR, Belgium), and Pine Needles  
333 SRM 1575a (from NIST, USA) were used to check the efficiency of both the acid digestion protocol

334 and the analysis. Data presented here are within 10% of deviation of recommended values for these  
335 international standards.

### 336 2.3. Statistical analyses

337 Results are shown as a mean of three replicates with standard deviation. Overall differences  
338 between sites in soil properties, stand and foliage biomass, foliar element concentrations, isotopic  
339 composition, stoichiometric ratios and resorption efficiencies were calculated using t-tests at  $P < 0.05$   
340 level, which were performed among sites for Gmelin's larch in permafrost terrain and between both  
341 species under the same conditions in the arboretum at each sampling date. Linear regression  
342 analysis was performed to examine the relationships between soil site characteristics, foliar  
343 mass-based nutrient concentrations, isotopic composition and carbon isotope discrimination. The  
344 resorption efficiency was calculated as

$$345 \quad \%RE = (N_{\text{green}} - N_{\text{sen}}) \times 100 / N_{\text{green}},$$

346 where  $N_{\text{green}}$  is the concentration of a nutrient in green needles collected before senescence in  
347 August, and  $N_{\text{sen}}$  is a nutrient concentration in senescent needles. All data treatments and statistical  
348 analyses were performed using STATISTICA ver. 6 (StatSoft Inc.).

## 349 3. Results

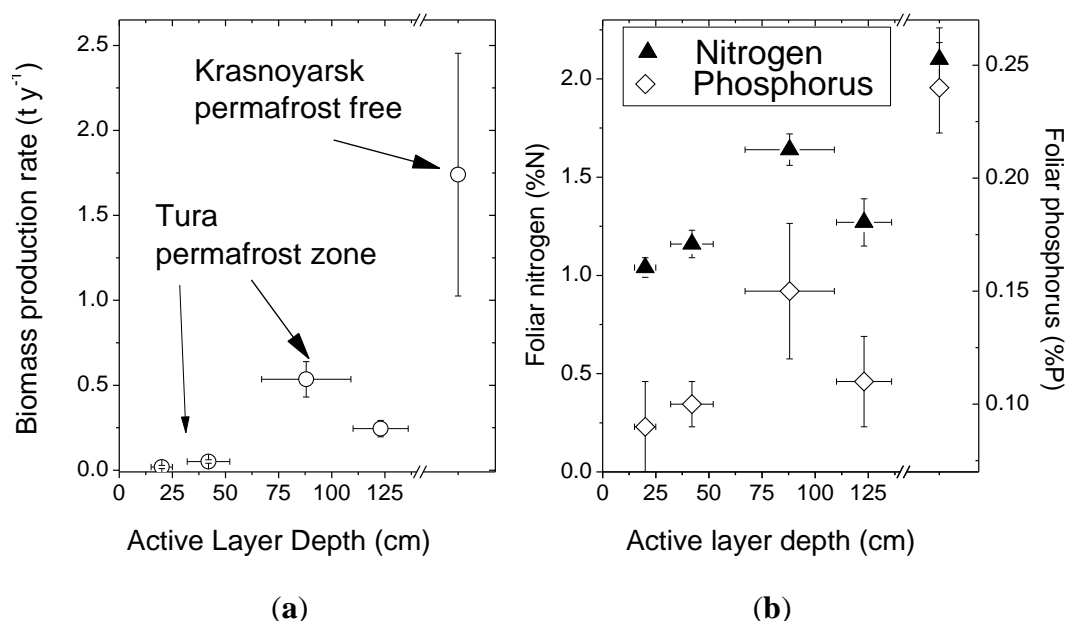
### 350 3.1. Tree and soil parameters

351 Permafrost and permafrost-free sites varied greatly in stand biomass (Table 1) taking into  
352 account the differences in the stand ages (>86 years vs. 32 years, respectively). Mean diameter, mean  
353 height and total biomass of the young larch stand in the permafrost-free site were comparable to  
354 156-year old intrinsically nutrient-rich riparian zone (TV) in permafrost terrain. Greater productivity  
355 of larch species in permafrost-free environment is also evident from 7- to 32-fold higher mean tree  
356 ring width (TRW) for both *Larix* species in Krasnoyarsk in comparison to larch trees of  
357 permafrost-affected sites. In the permafrost terrain at Tura, larch stands of similar age demonstrated  
358 also high inter-habitat variation. Mean tree diameter (DBH), height and tree-ring width differed  
359 about three-fold between *Sphagnum* plot (TB) and riparian zone (TV, Table 1). Stands developed on  
360 the slopes (TN and TS plots) were intermediate among those extremes, and higher growth of larch  
361 trees was found for the south-facing slope. Aboveground stand biomass had even larger differences  
362 among sites (>10-fold), i.e. 7-79 Mg/ha for total biomass and 0.2-7.0 Mg/ha for foliar biomass and  
363 increased with active layer depths (Figure 2a).

364 Carbon and nitrogen stocks in the upper 0.5 m of soil in different sites ranged from 3.3 to 11.9  
365 kg C/m<sup>2</sup> for total C and 0.3 to 0.5 kg N/m<sup>2</sup> for total N (Table 2), with a close positive correlation  
366 between C and N ( $r=0.92$ ,  $p<0.05$ ). The greatest values existed in permafrost terrain with the  
367 maximum amount of accumulated C and N in the soil of forested peat bog (TB, 11.9 kg C/m<sup>2</sup> and 0.5  
368 kg N/m<sup>2</sup>). The distribution of soil C and N between organic and mineral soil layers showed an  
369 increasing portion of organic layers with the severity of hydroclimatic conditions. In the in peat soil  
370 (TB site), the organic layer comprised more than 50% and 18% of the total C and N stocks.

371 Soil  $\delta^{15}\text{N}$  increased with soil depth and differed significantly among sampled sites: from +0.2 to  
372 -1.2‰ in organic layers and +1.6 to +3.4‰ in A horizons. Soil  $\delta^{13}\text{C}$  did not vary among sites, but  
373 increased slightly from organic layers (variation from -28.3 to -29.7‰) to the A horizons (-27.1 to  
374 -28.2‰).





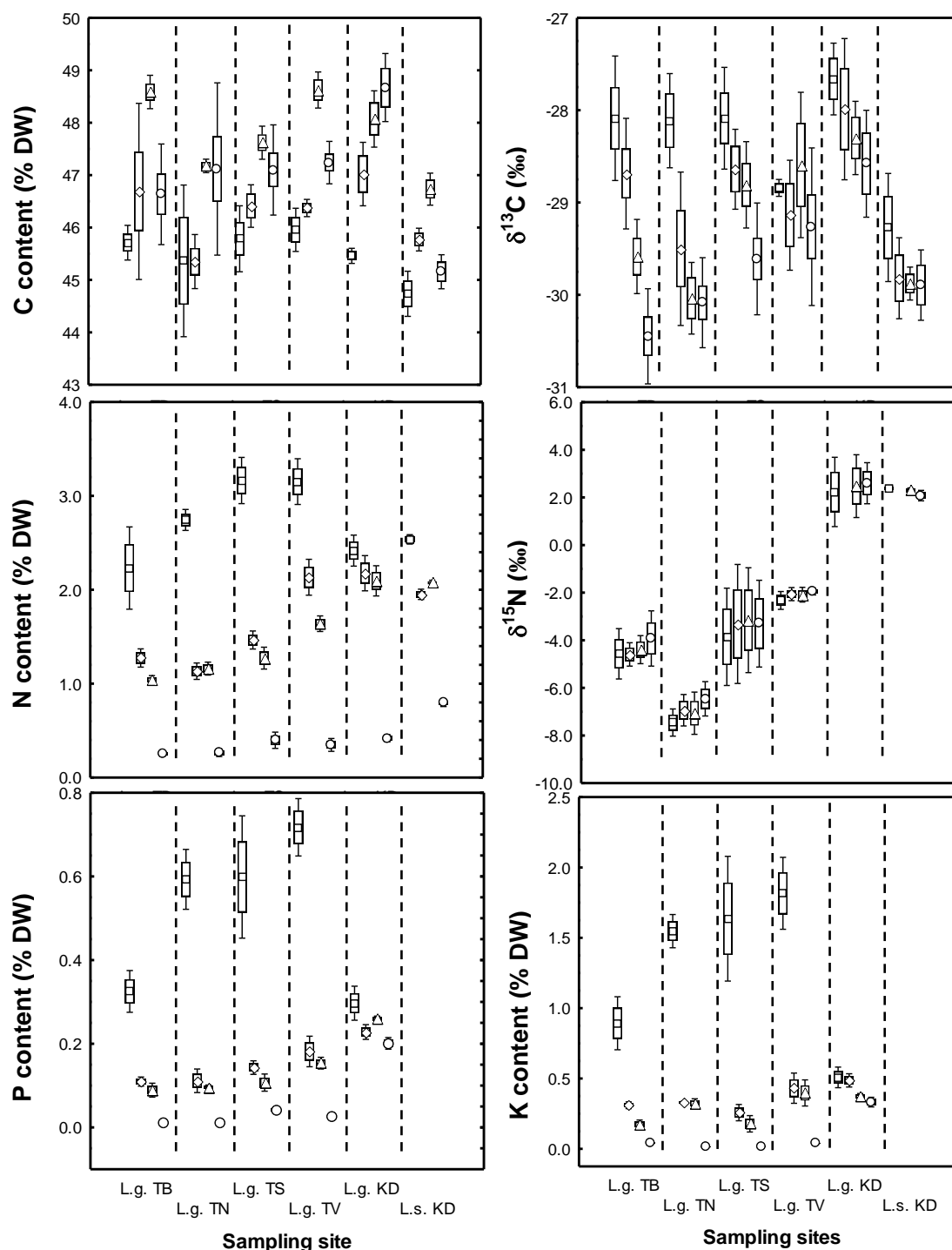
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376 **Figure 2.** Stand-specific stem biomass production rates of *Larix gmelinii* trees (a) and foliar N and P  
 377 concentrations in mature needles (August) in relation to respective soil active layer depth of the four  
 378 sites of the permafrost terrain and permafrost-free site (b).

### 379 3.2. Seasonal dynamics of foliar element concentrations and stable isotope composition

380 Needles of larch species in both sites show relatively similar patterns in the seasonal course of C  
 381 concentrations (Figure 3a) with a peak in August (46.7-48.7%) followed by lower concentrations  
 382 prior to abscission. The annual net gain of C in foliage calculated for individual trees (based on  
 383 allometric equations) ranged from 0.11±0.05 kg C/tree in the TB to 2.17±0.59 kg C/tree in the riparian  
 384 zone (TV). At the stand level, assimilated C in foliar biomass varied from 0.15 in TB to 3.40 t C/ha in  
 385 TV and reached 3.70 t C/ha in the permafrost-free terrain.

386 The  $\delta^{13}\text{C}$  values of larch foliage had highest values in juvenile needles and decreased during the  
 387 growing season in both permafrost and permafrost-free terrains, except for plot TV (Figure 3b).  
 388 Maximum depletion in heavy isotope during the season was up to 2-2.4 ‰, which was characteristic  
 389 for colder sites as TN and TB (ranged from -28.1 ‰ in June to -30.4 ‰ in September). To estimate leaf  
 390 carbon isotopic discrimination ( $\Delta_{\text{leaf}}$ ), the surrogate for water use efficiency (WUE<sub>i</sub>) by the equation  
 391 of Farquar et al. [32], we took mean -7.7 ‰ as the  $\delta^{13}\text{C}$  value in atmospheric CO<sub>2</sub> obtained in the  
 392 Zotino tall tower observatory (ZOTTO, 60 °N, 90°E) for June-August of 2008-2010 (SD = 0.3‰, range  
 393 -8.5 to -7.1 ‰). Carbon isotopic discrimination in juvenile larch foliage showed little variation  
 394 among permafrost habitats (21.2‰±0.4‰), but increased during the growing season by 1.5-2 ‰, as  
 395 opposed to ca. 1.2 ‰ enrichment of atmospheric CO<sub>2</sub> throughout the growing season. In August,  
 396 “colder” sites (TN and TB) had generally higher  $\Delta_{\text{leaf}}$ : (23.3‰±0.2‰) as compared to “warm” sites TS  
 397 and TV (22.0±0.4‰).  
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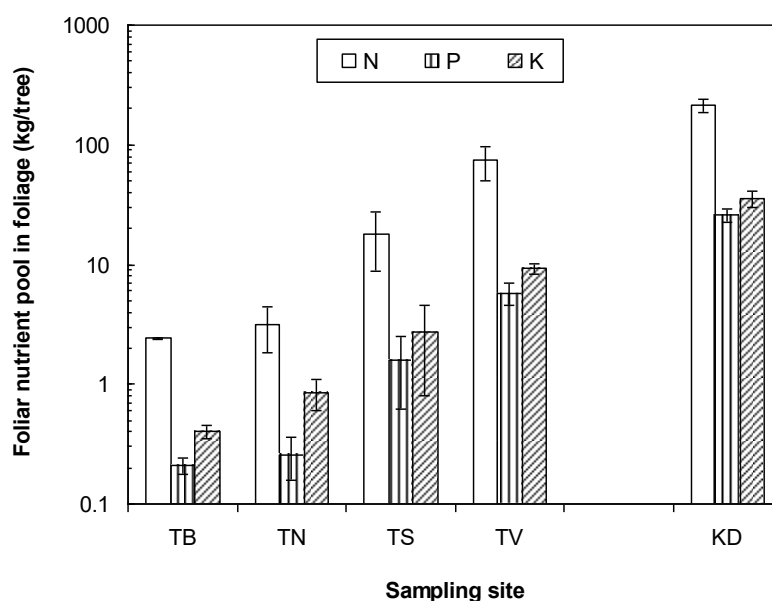
400 **Figure 3.** Seasonal evolution of mean contents of major elements (C, N, P and K) and stable isotope  
 401 composition ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) in needles of two larch species (L.g. – *Larix gmelinii*, L.s. – *Larix sibirica*) from  
 402 stands developed on continuous permafrost (Tura: TB – *Sphagnum* bog; TN – north-facing slope, TS –  
 403 south-facing slope, TV – riparian zone) and from a permafrost-free site (Krasnoyarsk: KD). Means of  
 404 3 replicate trees for different dates of sampling following phenological differences in Tura and  
 405 Krasnoyarsk, respectively: squares – 07.06.06 and 25.05.06, diamonds – 18.07.06 and 21.07.06,  
 406 triangles – 23.08.06 and 25.08.06, circles – 12.09.06 and 20.10.06. Box: mean $\pm$ SE; Whisker: mean $\pm$ SD.

407

408 Mass-based macronutrient (N, P and K) concentrations of larch needles showed also a typical  
 409 seasonal pattern (Figure 3c, e and f), which was more pronounced at the permafrost sites. Here,

410 nutrient concentrations in larch needles decreased by a factor of 2 to 9 from the early season until  
 411 July and August ( $p < 0.01$ ). “Warmer” sites in the permafrost zone had generally higher early season  
 412 macronutrient concentrations in needles ( $31 \pm 0.8$  mg N/g,  $6.0 \pm 1.5$  mg P/g and  $16.0 \pm 1.4$  mg K/g d.w.)  
 413 than larch trees growing in the *Sphagnum* bog ( $22 \pm 0.4$  mg N/g,  $3.3 \pm 0.5$  mg P/g and  $8.9 \pm 1.9$  mg K/g  
 414 d.w.) ( $p < 0.01$ ). In comparison to the permafrost site, seasonal changes of nutrient contents at the  
 415 permafrost-free soils (Krasnoyarsk) were negligible for P and K, and only a 10% reduction was  
 416 observed for N. As a result, the mid-summer nutrient contents in needles of Tura larches on  
 417 permafrost are around 50% lower than values found in trees growing on permafrost-free soils.

418 On a stand level N, P and K allocated in foliage of trees in permafrost-affected stands ranged  
 419 drastically among sites and increased with active layer depth (Figure 2b). Largest pools of nutrients  
 420 in foliar biomass were found in the permafrost-free terrain, following the order  $TB < TN < TS < TV < KD$   
 421 (Figure 4).



422

423 **Figure 4.** Nutrient pool/annual recruitment of major nutrients (N, P and K) in foliar biomass of  
 424 Gmelin’s larch in permafrost-affected (TB, TN, TS and TV) and permafrost-free sites (KD).

425 Foliar nitrogen stable isotope ratio ( $\delta^{15}\text{N}$ ) showed only little temporal variation during growing  
 426 season, but differed by as much as 9 ‰ among sites (Figure 3d). While the needles of permafrost-free  
 427 site had positive  $\delta^{15}\text{N}$  values of +2 ‰ in both *Larix* species, the north slope at Tura and the peat bog  
 428 had values of -7.0 ‰ and -5.0 ‰, respectively.

429 The C-to-N, N-to-P and C:N:P ratios from permafrost habitats showed an opposite trend  
 430 compared to mass-based concentrations of macronutrients. Elemental ratios were relatively narrow  
 431 at the beginning of the growing season, though 2-fold higher C:N:P ratio was observed in needles of  
 432 TB (Table 3). The C:N ratio ranged from ca. 15 in TS and TV to 18 and 22 in TN and TB, respectively  
 433 ( $p < 0.01$ ). The N:P ratio of juvenile needles showed certain differentiation among sites ranging from  
 434 4.7 in TN site to 6.8 in the TB with intermediate values shown for TS and TV sites. In comparison to  
 435 these values, Gmelin’s larch from Krasnoyarsk showed, at the same development stage, an N:P ratio  
 436 of 11 and C:N of 19. The N:P ratio increased during the growing season (up to  $12.0 \pm 0.2$  in August),  
 437 and showed surprisingly low variation between the sites. *L. gmelinii* from the permafrost-free site  
 438 showed an opposite trend, with N:P ratio decreasing from 11.1 (May) up to 8.3 (August). The C:N:P  
 439 stoichiometric ratio changed significantly in mid-season for the compared sites. Within the  
 440 permafrost region, needles from nutrient-poor and cold plots like TN and TB yielded generally  
 441 larger C:N:P ratios compared with nutrient-rich sites. By contrast, at the Krasnoyarsk site, the C:N:P  
 442 composition in Gmelin’s larch foliage was more narrow (190:8:1), and reflecting a slight enrichment  
 443 of nutrients in the mature foliage (Table 3).

444  
445**Table 3.** The dynamics of C:N:P ratio in foliage of *L. gmelinii* from different habitats in the permafrost region and the permafrost-free site.

Date of sampling	Permafrost-affected plots				Date of sampling	Permafrost-free plot
	TB	TN	TS	TV		L.g. KD
07.06.2006	144:6.8:1	77:4.7:1	78:5.4:1	71:4.8:1	31.05.2006	209:11.1:1
18.07.2006	440:11.7:1	421:10.5:1	327:10.3:1	293:13.4:1	20.07.2006	190:8.8:1
23.08.2006	557:11.9:1	493:12.1:1	451:12.0:1	335:11.3:1	25.08.2006	190:8.3:1
12.09.2006	4566:24.8:1	3227:18.0:1	1020:8.4:1	1236:8.9:1	20.10.2006	194:1.7:1

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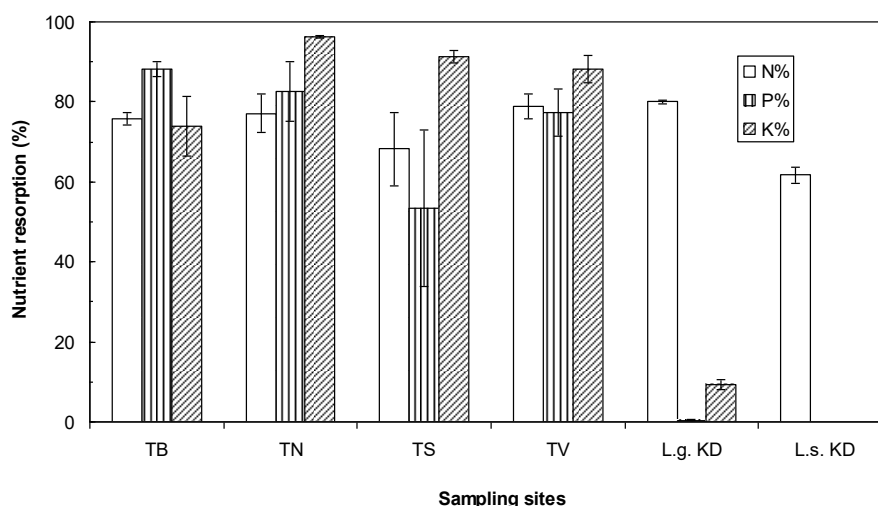
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Senescing needles showed an abrupt reduction of mass-based nutrient concentrations in comparison to the preceding sampling in August, but demonstrated a positive correlation with green tissues ( $r=0.97$  and  $0.96$  for N and P, respectively,  $p<0.01$ ). Analysis of species-specific nutrient resorption revealed that needles of *L. gmelinii* exhibited higher retranslocation of N to stem/branches prior to senescence when compared with *L. sibirica* (80% vs. 62%, respectively,  $p<0.05$ ) growing in the same plantation (Figure 5). The intra-species variation of resorption analyzed for *L. gmelinii*, growing in permafrost-free and permafrost sites, demonstrated relatively lower values in the latter case, ranging from 66% on the south-facing slope (TS site) to 79% in the riparian zone (TV). There was negligible resorption of P and K in senesced needles in foliage of *L. gmelinii* from the permafrost-free site. In contrast, when growing in permafrost-affected sites, this species showed significant ( $p<0.01$ ) withdrawal of both P (53–88%) and K (74–95%). In particular, needles from the north-facing slope had the highest resorption efficiency for K (96%), while the highest resorption for P (88%) was found for the peatbog site. As an average for permafrost terrain, the order of increasing nutrient resorption was  $K>P>N$  (84, 76 and 75 %, respectively). On the spatial basis, mean nutrient resorption decreased in the order  $TN>TV>TB>TS$  (85, 82, 79 and 72%, respectively). As a result of resorption, larch lost with needle litter only 19–25% of its nitrogen, 12–47% of its P and 5–27% of its K.



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**Figure 5.** Mean intra- and inter-species variation of nutrient resorption efficiency of larch species from a permafrost-affected (Tura) and permafrost-free (Krasnoyarsk) sites. Resorption of P and K is not available for *L. sibirica* (L.s. KD) as these elemental concentrations were not measured in senesced needles.

468

#### 4. Discussion

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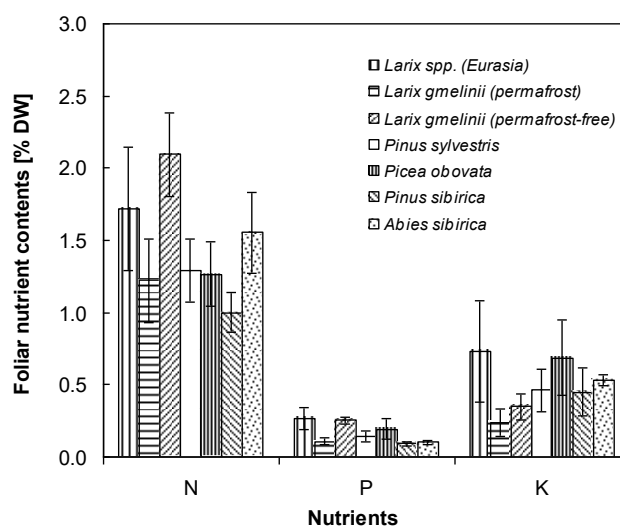
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Our study along a gradient in permafrost regime in Central Siberia showed that (1) the nutritional status of larch trees reflected by the concentrations and pools of macro nutrients strongly

471 improved with the depth of the active layer which goes along with increased tree productivity. (2) In  
 472 permafrost soils, we also observed a strong temporal dynamics in needle nutrients with a high  
 473 resorption in autumn and a high nutrient investment into juvenile needles which might be a strategy  
 474 of larch to become photosynthetically highly active despite frozen soils early in the season. (3)  
 475 Finally, increasing needle  $\delta^{15}\text{N}$  values with increasing active layer depth strongly suggests that  
 476 cycling of N and possibly other nutrients will accelerate with permafrost melt which likely  
 477 contributes to an increasing productivity of larch stands in Siberia.

#### 478 4.1. Nutrient status of larch improves with active layer depth

479 The mass-based concentrations of major nutrients in needles of *Larix* spp. in mid-growing  
 480 season observed in this study are in the lower range of reported values for Eurasia and Northern  
 481 America [5,9,12,25](Figure 6). At the permafrost site at Tura, concentrations of N, P and K in mature  
 482 needles were 50% less than the optimum contents of major nutrients in larch needles (2.1-2.6% for N,  
 483 0.3-0.6% for P and 0.9-2.0% for K) reported by [12]. Along the gradient in permafrost regime, the  
 484 macronutrient concentrations in larch foliar biomass increased with increasing active layer depth  
 485 reflecting improving site conditions (site fertility index or “bonitet” in Russian system). This increase  
 486 was also reflected in a higher productivity of larches under favorable conditions, strongly  
 487 suggesting that an improving nutrient availability contributes to the growth enhancement with  
 488 increasing depth of the active layer.



489

490 **Figure 6.** Mass-based concentrations of macronutrients in the foliage of main conifers of Siberia  
 491 during the mid-growing season [12] compared with *L. gmelinii* collected at permafrost-affected and  
 492 permafrost-free sites in this study.

493 Our data also suggest a threshold level of nutrient content in mature larch needles from this  
 494 environment (ca. 1% for N), below which trees are likely to decline. On the other hand, larches from  
 495 all permafrost-affected sites have a relatively narrow range of nutrient concentrations in foliage (e.g.  
 496 1.0-1.6% N) despite a 10-fold difference in overall standing stock and 25-fold difference of needle  
 497 biomass between site with a shallow and a deep active layer depth. This pattern implies that an  
 498 improving nutrient availability in the soil is rather reflected in aboveground biomass increment and  
 499 in total nutrient uptake than in increased foliar nutrient concentrations. The gradient in nutrient  
 500 availability among sites is probably also reflected in C allocation among below- and aboveground  
 501 biomass. For our study region, Kajimoto et al. [33] reported that the poorly-drained and colder soils  
 502 TB peatland site has 2-fold higher root-to-shoot ratio (1.13) in comparison to sites with larger active  
 503 layer thickness (i.e. < 0.5). Such patterns are mainly explained by an increasing competition  
 504 belowground for accessible resources within a limited soil volume.

505 Foliar stoichiometric ratios like N:P or C:N are reported as a good predictors of nutritional state  
506 of plants in nutrient-limiting environments [9,24]. At the plant level, N:P ratios of <14 and >16  
507 corresponds to N- and P-limited biomass production, respectively, as demonstrated by fertilization  
508 experiments [16,24, 34]. However, the Eurasian data set for *Larix* needles by Girs [12] shows average  
509 N:P ratios of 6.5, which suggests a general N limitation of larch growth throughout Eurasia. In our  
510 study, N:P ratios increased from 4-6 in juvenile needles to 10 later in the growing season (Table 3),  
511 indicating that *Larix* is principally N limited but to a lesser extent than in other regions of Eurasia.  
512 The very small N:P ratio early in the season might not be indicative for a N limitation as N  
513 concentrations were very high with values of 3%. Interestingly, N-P ratios of the various sites within  
514 the permafrost region were very similar suggesting that they have similar physiological traits and/or  
515 adaptation to cold soils.

#### 516 4.2. $^{15}\text{N}$ enrichment of needles on warmer soils

517 In larch stands of the studied permafrost region, N-pools varied from 0.2 to 1.0 Mg N/ha in the  
518 organic soil layers [35], and an additional 3.3-5.2 Mg N/ha (this study) or up to 6.6 Mg N/ha [36] in  
519 the mineral soil. Overall, the soil nitrogen pool usually exceeds 80% of the total ecosystem N pool in  
520 northern taiga [37]. Nevertheless, the availability of N and other nutrients for plants is limited due to  
521 small net N mineralization rates and plant growth largely depend on nutrient supply provided by  
522 ECM fungi. Hobbie and Högberg [38] reported that mycorrhizal fungi provided 61-86% of the  
523 N-uptake for arctic tundra plants and for Alaskan permafrost terrain and Mayor et al. [39] estimated  
524 that ECM-derived N may constitute 8-92% of black spruce annual demand. Our results showed that  
525 larches growing on deep active layers with smaller total soil N stocks had higher foliar mass-based  
526 N concentrations and elevated  $\delta^{15}\text{N}$  values. The strong enrichment with  $^{15}\text{N}$  in 'warmer' soils is  
527 indicative for an improved N supply [40, 20]. A soil warming study at the alpine treeline with *Larix*  
528 suggests that increased  $\delta^{15}\text{N}$  values are related to increased contents of mineral N in the soil, which  
529 reduced the need to take up N via mycorrhiza which in turn induces  $^{15}\text{N}$  depletion in foliar biomass  
530 [41]. Alternatively,  $^{15}\text{N}$  enrichment may reflect N-uptake from the deeper unfrozen soils which are  
531 enriched in N as compared to the topsoil. The peat bog was an exception in this pattern with larches  
532 having higher foliar  $\delta^{15}\text{N}$  values (ca. -5.0 ‰) in comparison to the north-facing slope. One reason  
533 could be a decreasing abundance of ECM fungi in bogs, because they are sensitive to waterlogging  
534 and P-limitation [42] and a consequence, larches in bog rely more strongly on mineral N. Except the  
535 peat bog, N concentrations and  $\delta^{15}\text{N}$  values correlated positively with larch productivity, which  
536 strongly suggests that an improving N nutritional status with increasing depth of the active layer is  
537 an important driver for the better tree growth in warmer soils.

#### 538 4.3. Strong seasonal dynamics in nutrient concentrations and $^{13}\text{C}$

539 At the permafrost site, nutrient concentration showed a very strong seasonal variation with  
540 several fold decline throughout the growing season. The highest concentrations of foliar N, P and K  
541 at all permafrost-affected sites were found in the early growing season, when the needles were first  
542 produced. A similar pattern was reported for the same elements in Siberian larch from Mongolia [9]  
543 and micronutrients (i.e. Cu, B, Na, Ni etc.) in the same habitats for Gmelin's larch [30]. Elevated N, P  
544 and K concentrations are indicators of active metabolic processes and high photosynthetic rates (i.e.  
545 high Rubisco content) as well as high energy requirements and protein synthesis [43]. In our study,  
546 the initial peak in nutrient concentrations was much less pronounced at the warmer permafrost-free  
547 sites, suggesting that low temperatures are reinforcing this pattern. In support, Woods et al. [44] as  
548 well as Reich and Oleksyn [25] interpret the enrichment in foliar nutrients (mainly N and P) as an  
549 adaptation by plants to enhance metabolic activity and growth rates under low temperatures [25,44].  
550 Remarkably, the highest concentrations of macro- and micronutrients in larch foliage of  
551 permafrost-affected sites occurred when the soil remained frozen and the uptake of nutrients from  
552 the soil was very limited. This indicates that the development of the photosynthetic apparatus in the  
553 early season is based on the large pool of nutrients accumulated during the previous growing season  
554 and stored throughout the winter. The substantial translocation of nutrients in larch needles from

555 year to year in permafrost terrains is supported by our findings of a strong resorption of nutrients in  
556 the permafrost sites but not on permafrost-free soils. Resorption is a key mechanism for deciduous  
557 plants to avoid losses of essential nutrients towards litter [24]. It is hypothesized to be particularly  
558 high at nutrient-poor sites [16] supplying a considerable proportion of a tree's nutrient requirement  
559 for new biomass production [24, 25]. The recycling of nutrients is even more essential for trees that  
560 renew their foliar on annual basis and which thus, require large quantities of C and nutrients to  
561 construct new photoassimilating biomass. Our results show that permafrost is even fostering  
562 nutrient resorption to support tree's life early in the following year.

563 We observed that juvenile needles were enriched in  $^{13}\text{C}$  as compared to mature needles, which  
564 could indicate that storage carbohydrates (e.g. starch) that are generally more enriched in  $^{13}\text{C}$  served  
565 as essential C source in early developmental stages [9]. However, also higher photosynthetic rates  
566 (and respective reduction of  $c_i/c_a$  ratio) under high foliar N and P levels may also lead to elevated  $^{13}\text{C}$   
567 in early season foliage of larch.

568 With the progression of the growing season bulk foliar  $^{13}\text{C}$  decreased probably reflecting an  
569 increasing of proportion of current photoassimilates used for needle growth [9]. In addition, nutrient  
570 concentrations decreased strongly, which is typical for N in deciduous angiosperm species and  
571 evergreen conifers [12,45]. Much less marked changes are usually observed for foliar P and K,  
572 although some authors report their similar dynamics to N [46]. Likewise, nutrient concentrations in  
573 larch needles from the permafrost site changed predictably as a function of needle development and  
574 the needle C:N, C:P and C:K ratios increased significantly with needle maturation. Firstly, the foliar  
575 nutrients become diluted by increasing quantities of C-rich cell-wall material [26]. Higher  
576 lignification of needle tissues in nutrient-poor environments may further enrich needles in C-rich  
577 aromatic compounds [47], which might be indicated by the findings of lower  $\delta^{13}\text{C}$  values in bulk  
578 needles as lignin is generally depleted in  $^{13}\text{C}$ . Another reason reported for decrease of nutrients  
579 during a growing season is nutrient withdrawal to active growing zones (e.g. fine roots, shoots)  
580 and/or reproductive organs of plants growing on nutrient-limited soils [45,48].

## 581 5. Conclusions

582 Our results indicate that on permafrost soils, the preservation of macronutrients by resorption  
583 during autumn and the formation of juvenile needles with very high nutrient contents and  
584 particularly low N:P ratios at the beginning of the growing season is an important mechanism of  
585 larch trees to sustain a high metabolic activity early in the season, despite low air temperatures and  
586 frozen soils. Such a strategy may allow larch forests to cope with a low nutrient availability in cold  
587 soils in the short-term early in the season or even in the long-term for the entire life-span of trees  
588 where the development of thick soil-insulating organic layer induces a progressive nutrient  
589 limitation.

590 Our site comparison showed that with increasing active layer depth nutrient contents,  $\delta^{15}\text{N}$   
591 values and biomass productivity strongly increased. This pattern implies that deepening of soil  
592 active layer increases rates of nutrient cycling in soils which in turn stimulates the productivity of  
593 larch forests over vast permafrost regions of Siberia. Consequently, permafrost degradation by  
594 climatic warming may enhance the currently weak sink of atmospheric  $\text{CO}_2$  in these landscapes  
595 (e.g. NEP = 76  $\text{gC/m}^2/\text{a}$  reported for Tura site [11]) if it is not outbalanced by increased  $\text{CO}_2$  losses  
596 from soil organic matter which is so far locked in permafrost. An increased NEP can be expected as  
597 long as tree productivity is supported by an enhanced nutrient availability. Closely similar foliar N:P  
598 ratios observed in different sites of the permafrost region, contrasted with N:P ratio variation in  
599 permafrost-free sites, which suggests site-specific metabolic traits of Gmelin's larch and/or  
600 site-specific nutrient availability at local climatic and soil conditions. Along with site-specific  
601 resorption efficiency for these elements the observed patterns indicate that in permafrost terrains of  
602 the Central Siberian Plateau not only N, but also P and K may currently limit tree growth.  
603 Particularly, the higher efficacy of P and K resorption in poor and cold habitats reflects the plasticity  
604 of larches to maintain growth in severe environment.

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 609 designed and performed the experiments. ASP, FH, OSP, MPP, JV and WHM analyzed the data and  
 610 wrote the manuscript.

611 **Conflicts of Interest:** The authors declare no conflict of interest.

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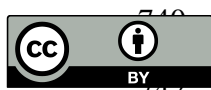
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