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How do soil properties affect alpine treelines? General principles in a global perspective and novel findings from Rolwaling Himal, Nepal

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Abstract

Little is known about how soil properties control tree growth at its upper limit. This paper reviews the state of knowledge and discusses the results specifically related to ecozones, to the scale-dependent importance of single factors, and to new findings from a near-natural treeline ecotone in Rolwaling Himal, Nepal. This paper identifies gaps in literature and shows where new research is needed, both conceptual and geographical. The review shows that at a global scale and throughout diverse ecozones, growing season soil temperature is considered a key factor for tree growth. Soil temperatures differ greatly at a local scale, and are mainly determined by local climatic, edaphic, and topographic conditions. Our result of $7.6 \pm 0.6°C$ for growing season mean soil temperature at treeline in Rolwaling is 1.2 K higher compared to the postulated $6.4 \pm 0.7°C$ for alpine treelines. We suggest a broadening of the $\pm 0.7°C$ error term to cover the wide range at a local scale. The role of major soil nutrients and soil moisture for treeline shift has been underestimated by far. In Rolwaling, significantly decreasing nutrient availability (N, K, Mg) in soils and foliage with elevation might explain why treeline shift and global warming are decoupled. Further, soil moisture deficits early in the year impede seedling and sapling establishment, which could be an important mechanism that controls treeline position. These findings question previous results which argue that alpine treelines are unaffected by soil nutrient availability and

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soil moisture. We assume that specific combinations of soil properties as well as single soil properties limit tree growth even below climatic treelines.

I Introduction

Soil properties play a major role for plant growth. Since Liebig's law of the minimum it is known that plant growth is ruled by the amount of the most limiting soil nutrient, and not by the total amount of available soil nutrients. Alpine treeline ecotones are characterized by extreme climate conditions and very limited resources (Holtmeier, 2009; Körner, 2012; Wieser and Tausz, 2007). In this respect, they can be regarded as model systems that deepen our understanding to what extent limitations in essential soil nutrients, plant available water, and soil temperature control tree growth and tree recruitment. Results of alpine treeline ecotone research can explain how these factors modulate not only the general altitudinal position of a treeline (m a.s.l.), but also relative differences in elevation and form (diffuse, abrupt, krummholz, island; according to Harsch and Bader, 2011) at a local scale. In this study, we investigate the effects of soil properties on alpine treelines, simplified by using the term 'tree growth'.

Within the altitudinal zonation of vegetation in high mountains, the upper treeline (for detailed treeline terminology, see Holtmeier, 2009; Körner, 1998a, 2003a, 2012) is the most visible physiognomic boundary and at the same time one of the most fundamental ecological boundaries. It represents a significant limit in the continuous change of ecological conditions with elevation, expressed by more or less abrupt alterations of dominating life forms and plant communities. While investigating alpine treelines, it is essential to distinguish between different spatial scales (Wilbanks and Kates,

1999). This is especially important with regard to soil properties in treeline ecotones, which largely reflect soil formation as a function of climate, biota, topography, parent material, and time under natural conditions (e.g. Jenny, 1941). At a global scale, it is commonly assumed that tree growth at its upper limit is controlled by temperature, i.e. insufficient air and soil temperatures during growing season (e.g. Holtmeier, 2009; Körner, 1998a, 1998b, 2007, 2012; Körner and Paulsen, 2004; Wieser and Tausz, 2007). The general agreement of a thermal limitation may not, however, hide the fact that there is an ongoing controversial debate on the relevance of various specific abiotic and biotic drivers (e.g. carbon and nitrogen uptake and investment, soil nutrient availability, plant available water, geology and geomorphology, species dispersal and recruitment, plant morphology, self-organization), which influence tree growth at its upper limit (e.g. Hoch and Körner, 2003, 2009; Holtmeier and Broll, 2007, 2010; Macias-Fauria and Johnson, 2013; Smith et al., 2003; Sullivan et al., 2015; Weih and Karlsson, 2001).

The current state of knowledge on treelines has been attained by a great variety of research at different spatial scales (see Malanson et al., 2011). At a global scale, studies exploring general causes of treelines are often characterized by a strong focus on limitations to tree growth from an ecophysiological perspective (e.g. Harsch et al., 2009; Holtmeier, 2009; Körner, 1998a, 1998b, 2003a, 2007, 2012; Körner and Paulsen, 2004). Another cluster of studies attempt to understand finer-scale causes of treelines and focus in particular on the effects of topography and other site conditions, and on

treeline history (e.g. Gehrig-Fasel et al., 2007; Liptzin et al., 2012; Loomis et al., 2006; McNown and Sullivan, 2013; Treml and Banaš, 2008). As the treeline heterogeneity increases from a global scale to a local scale, an increasing number of factors and their interactions have to be considered when analyzing the mechanisms locally.

Thus, the global approach is appropriate when the focus is on deducing general principles concerning soil properties and their relation to tree growth in treeline ecotones. The local approach is considered appropriate when analyzing complex effects of small-scale varying soil properties on tree growth in treeline ecotones, all the more when considering that specific combinations of soil properties as well as single soil properties may limit tree growth even below climatic treelines. Analyzing relationships between soil properties and treeline spatial patterns is impeded by the fact that many treelines are strongly affected by human impact today (Holtmeier, 2009; Miehe and Miehe, 2000; Schickhoff, 2011), and that recent treeline dynamics are largely the result of historical and modern land use effects (Gehrig-Fasel et al., 2007; Holtmeier and Broll, 2007). In general, negative effects of soil temperatures on tree growth are well documented while soil properties such as plant available water, soil nutrient availability, and soil physical properties rarely appear in literature. Research on the effects of soil properties on tree growth at its upper limit is rather descriptive than quantitative. Also, several regions (e.g. Himalaya) are highly underrepresented in treeline literature. Himalaya has been identified as an important region, which unfortunately has not yet gained the appropriate amount of attention. Global warming might actually affect this region to a greater extent than it affects other treeline ecotones (Schickhoff, 2005). The results in this article from Rolwaling Himal, Nepal will help fill these gaps.

Summarizing, we follow three approaches in this paper:

1. We review how soil properties affect tree growth at its upper limit and infer general principles in a global perspective.
2. We identify regions and soil variables that have not gained adequate attention yet. From this, we indicate important advances needed in the field of treeline research.
3. We analyze the role of soil properties for tree growth at a local scale based on recent research results from a near-natural treeline ecotone in Rolwaling Himal.

II Research Design and Methodology

We used the literature databases Web of Science (WOS) and Bielefeld Academic Search Engine (BASE) to search for alpine treeline-related literature. The search terms were "treeline", "tree line", "tree-line", "alpine treeline", "soil treeline", "treeline tree growth", "timberline", "timber line", "mountain timberline", "soil timberline", "timberline tree growth", "forestline", "forest line", "forest-line", "soil forestline", and "forestline tree growth". These terms were all used in independent searches, which resulted in 507 published treeline studies (see Appendix S1 in online supplementary data). A literature review of these studies reveals the importance of various treeline-controlling factors as well as underlying processes, and subordinate factors at different spatial scales (cf. Table 1).

In this review, we carried out a five-category rating of treeline-controlling factors as listed in Table 1, which is based on the findings of the respective author(s). In case the explanatory power of potential factors was evaluated by the author(s), we followed their ranking of factors and converted them into five categories. In all other cases, we assigned their findings into five categories graduating the factors from a very high to very low effect on tree growth at its

Table 1. Factors, underlying processes and subordinate factors controlling tree growth at its upper limit, and their spatial relation. Factor categories were modified according to Case and Duncan (2014).

Factor	Factor category	Processes and subordinate factors	Spatial scale
Temperature	Direct thermal limitation/thermal modifier	Heat deficiency, continentality, mountain mass effect, cold air ponding in valleys, winter desiccation, freezing damage, temperature extremes, etc.	Global, local
Soil temperature	Direct thermal limitation/thermal modifier	Heat deficiency, impaired root and stem growth, permafrost, frost drought, etc.	Global, local
Soil moisture	Direct limitation/ physiological stressor	Plant-available water supply, drought, nutrient leaching, etc.	Local
Length of growing season	Thermal modifier/ physiological stressor	Latitudinal effect, snow cover and depth, etc.	Global, local
Precipitation/ humidity	Thermal modifier/ physiological stressor	Water supply, drought	Local
Sun exposure	Thermal modifier/ physiological stressor	Solar radiation intensity, heat loading	Local
Soil physical properties	Physiological stressor	Soil forming processes, soil depth, soil texture, bulk density, etc.	Local
Nutrients	Physiological stressor	Soil chemical properties (e.g. nutrient availability, soil pH, base saturation, ion exchange), soil fauna (mycorrhizal symbiosis, microorganisms), nutrient uptake and investment by trees, foliar nutrients, etc.	Local
Carbon balance	Physiological stressor	Carbon limitation, low CO_2 partial pressure, tree carbon uptake and investment	Local
Wind	Physiological stressor	Breakage, removal of foliage, rime ice, removal of snow	Local
Vegetation/tree species	Physiological stressor	Architecture, reproduction, germination, seed dispersal and establishment, regeneration, plant morphology, self-organization, competition	Local
Human impact	Physiological stressor	Fire, pastoral use, forest use, tourism, site history, soil compaction, soil erosion	Local
Animals	Physiological stressor	Trampling, insect infestations, pathogens, diseases	Local
Geology	Physiological stressor	Parent material	Local
Topography	Disturbance	Landslides, snow avalanches, earthquakes, etc.	Local

upper limit. For example, statements like "tree growth is constrained by growing season mean soil temperature" were assessed as very high, "tree growth is limited by heat deficiency and low precipitation" as high, respectively, or "tree growth is not affected by carbon limitation" were assessed as very low, etc. In some cases, more than one treeline-controlling factor

from a given paper was being tallied in the same category. We weighted the number of tallies in the respective categories by multiplying with 5 (very high), 4 (high), 3 (medium), 2 (low), and 1 (very low) to increase the discriminatory power of the evaluation. The results were summed up for each treeline-controlling factor and divided by the total number of tallies for the respective factor to characterize its importance (equation (a)). To account for the relative importance of a single factor in relation to all other factors, and to avoid overestimation of importance of factors with a low number of total tally, the importance of a treeline-controlling factor was multiplied by the quotient of the total number of tallies per treeline-controlling factor and the total number of studies reviewed (507) (equation (b)). Finally, the values were standardized to 100% (equation (c)).

$$\textit{Index } [1] = \frac{c1 \times 5 + c2 \times 4 + c3 \times 3 + c4 \times 2 + c5 \times 1}{\sum c1 + \ldots + c5} \quad \text{(a)}$$

$$\textit{Index } [2] = \textit{Index } [1] \times \frac{\sum c1 + \ldots + c5}{\sum n} \quad \text{(b)}$$

$$\textit{Relative importance } [\%] = \left(\frac{\textit{Index } [2]}{\sum \textit{Index } [2]} \right) \times 100 \quad \text{(c)}$$

with c = number of tallies per category, n = total number of studies.

The same calculations were applied to single ecozones to analyze the relative importance of factors for tree growth in the respective ecozone. Ecozones were classified by using the subdivision of Körner (2012). In addition, we quantified what responses have been at treeline to soil-related factors (see Appendix S2 in online supplementary data).

To question the results of prior studies, we evaluated data from our own fieldwork in the TREELINE project in Rolwaling Himal. The study area is located in the northeast part of Central Nepal on a north exposed slope reverse to the small Sherpa village of Beding (N 27°54′, E 86°22′; Figure 1). The climate is characterized by dry, cold winters, and is dominated by the monsoon in summer months (June–September). As soil types, we found exclusively podzols (IUSS Working Group WRB, 2006) which indicate a strong vertical translocation of soil organic matter and sesquioxides (primarily Al, Fe) at very low soil-pH (2.5–4) with soil depth (leaching). The krummholz-formed near-natural treeline is situated at 3900–4000 m a.s.l. The mean tree height of treeline trees is 5–6 m. Human impact in the treeline ecotone is negligible, merely small areas in the lowest parts of closed forest (adjacent to the left bank of the river near the valley bottom) are affected by marginal deforestation from local people for firewood usage who live right bank of the river. Our case study investigated local scale conditions; however, we claim that it is representative for a larger region.

Within the TREELINE project, we use a stratified random experimental design with three transects ($2\times$ NE exposed slopes, $1\times$ NW exposed slope; Figure 1) divided into four altitudinal zones: A (closed forest), B (uppermost closed forest), C (krummholz belt), and D (dwarf shrub heath). Within each zone of each altitudinal transect, four different plots (20 m $\times$ 20 m) were randomly selected. In total, 48 plots were sampled (3 transects $\times$ 4 altitudinal zones $\times$ 4 plots) for soil, litter, and decomposition layer, as well as foliage from evergreen tree species *Abies spectabilis* and *Rhododendron campanulatum*, from evergreen dwarf shrub species *Rhododendron anthopogon* and *Rhododendron setosum*, and from deciduous tree species *Sorbus microphylla*, *Betula utilis*, and *Acer caudatum*. Samples were taken at the onset and end of vegetation period in 2013 and 2014.

Soil and decomposition layer samples were analyzed for carbon (C), nitrogen (N), plant available nitrogen (Nmin), effective cation exchange capacity (Na, K, Mg, Ca, Mn, Fe, Al), and pH value. For litter and foliage, nutrient concentrations (C, N, Na, K, Mg, Ca, Mn, Fe, Al) were measured. C and N of all samples were
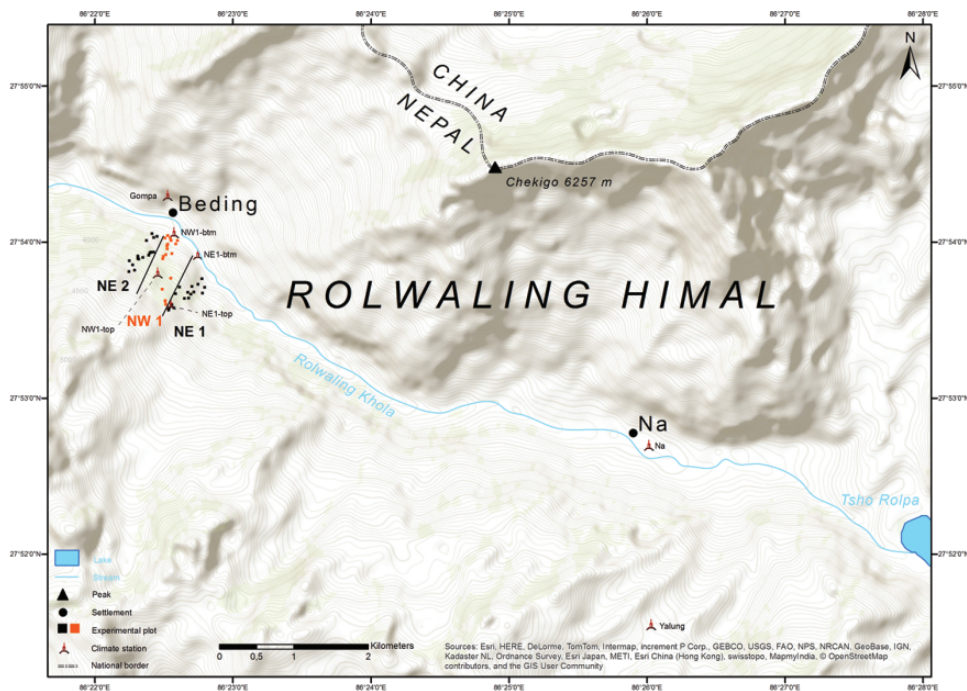
Figure 1. Study area and experimental design. Experimental design includes three investigated altitudinal transects (NE1, NE2 = northeast aspect (black), NW1 = northwest aspect (red)), and location of experimental plots and climate stations (btm = bottom; top; Gompa; Na; Yalung).

determined using *elemental analyzer vario EL II*. For analysis of Nmin (NO_3^-, NH_4^+), an aliquot of 10 g of homogenized field-fresh soil material with 50 mL 1 M KCl solution, shaking vigorously every 15 minutes for one hour. The extraction solution was filtered, and subsequently acidified with HCl. Nmin fractions were analyzed in the laboratory by continuous flow analysis (*CFA, SEAL Auto Analyzer AA3 HR)*. Effective cation exchange capacity of soils and decomposition layers was analyzed using inductively coupled plasma optical emission spectrometry (*ICP-OES, Perkin Elmer Optima 5300 DV)*. Litter and foliage samples were measured with *ICP-OES* after microwave-digestion (*MLS START 1500 Microwave Extractor*; application E208 – plants low acidity: 4 mL HNO_3, 3 mL H_2O_2, 5 mL H_2O). pH values of soils and decomposition layers were detected electrometrically in 1 M KCl and in distilled H_2O at a ratio of 1:2.5 using combination electrode and pH meter (*WTW ProfiLine pH 3310*). Additionally, 32 modified Wi-Fi plant sensors (Koubachi AG) were installed along two altitudinal transects (2 transects (NE2, NW1) $\times$ 4 altitudinal zones $\times$ 4 plots) to measure temperature at the soil surface and in 10 cm soil depth, and soil moisture (pF = decadic logarithm of the absolute value of soil water tension; non-dimensional) in 10 cm soil depth, in a 1 hour interval. These sensors were modified for outdoor usage to log soil temperatures from $-10°C$ to $+55°C$, and pF from 0 to 5.75 in various temporal resolutions. We use lithium batteries which ensure energy supply under harsh climatic conditions. Data were obtained via a Wi-Fi interface. Based on pF, soil texture (DIN ISO 11277), soil bulk density (DIN ISO 18126), and soil volume (dm m^{-2}), we calculated soil available water capacity (AWC; L dm^{-1} m^{-2}).

With regards to spatial distribution of soil and foliar nutrients, and spatial and temporal distribution of soil temperature in the Rolwaling treeline ecotone, statistical analyses were accomplished with the free programming language R, version 3.1.2 (R Development Core Team, 2014) using packages *car* (Fox and Weisberg, 2011) and *PMCMR* (Pohlert, 2014).

III Results and discussion

1 Treeline-controlling factors

Heterogeneity of treelines in terms of physiognomy and ecological settings suggests that the treeline is induced and shaped by diverse factors and factor complexes, which vary in space and time (extensively reviewed in Holtmeier, 2009; Körner, 2012). Treeline-controlling factors can be assigned to superordinate categories such as climatic variables, topography, soils, tree species, biotic influences, and human impact. However, the interactions of treeline-controlling factors are not yet fully understood, and relationships between factors are generally complex (e.g. Holtmeier, 2009; Körner, 1998a, 2012). Some factors have possible direct negative effects on tree growth (e.g., temperature, moisture limitation), while others have indirect effects or actually are proxies for direct effects (e.g., topography, sun exposure, vegetation). Following this, Harsch and Bader (2011) and Case and Duncan (2014) provide conceptual frameworks for how different factors may impact the treeline. As shown in Table 1, Case and Duncan (2014) identify three types of factors (thermal modifiers, physiological stressors, and disturbance factors) that can affect treelines at different scales. Further, historical influences often affect present-day treeline patterns and have to be considered as well for causal explanations.

The majority of global studies are observation studies or reviews mostly summarizing studies conducted at finer scales (referred to as local), and seek for a general explanation
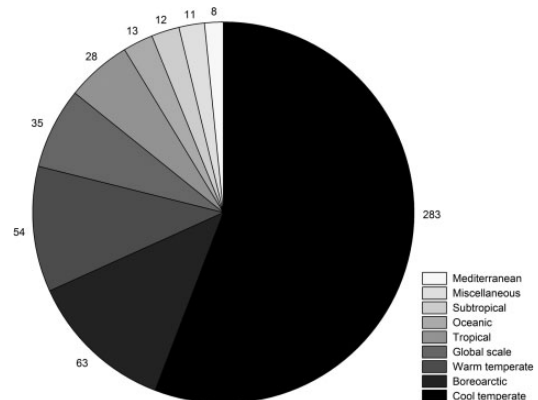

Figure 2. Reviewed treeline literature ($n = 507$) according to the investigated ecozone ($n = 472$) related to global scale studies ($n = 35$). Finer-scale studies are distinguished into seven different ecozones (boreoarctic, cool temperate, Mediterranean, oceanic, warm temperate, subtropical, and tropical). Miscellaneous: some studies include different spatial scales, which cannot be separated.

of the treeline phenomenon. Local studies are often based on measurements or experiments (e.g. soil warming), vary substantially in their focus, and investigate a causal explanation for the limitation of tree growth at a finer scale predominantly. Most global studies ($n = 35$; Figure 2) focus on tree growth limitation from an ecophysiological perspective, whereas local studies ($n = 472$) focus in particular on the effects of microclimate, topography, or treeline history. Our review also reveals that the number of studies in some ecozones (especially subtropics, Mediterranean and oceanic islands) is too little to understand the constraints on tree growth in such regions and to relate those to findings in other ecozones or in a global perspective.

Overall, the results show that air temperature is assumed to be the most important treeline-controlling factor, both at a global and a local scale (Figure 3(a)). The term air temperature affecting tree growth in general includes growing season mean air temperature, and minimum air temperature thresholds. In the following, we
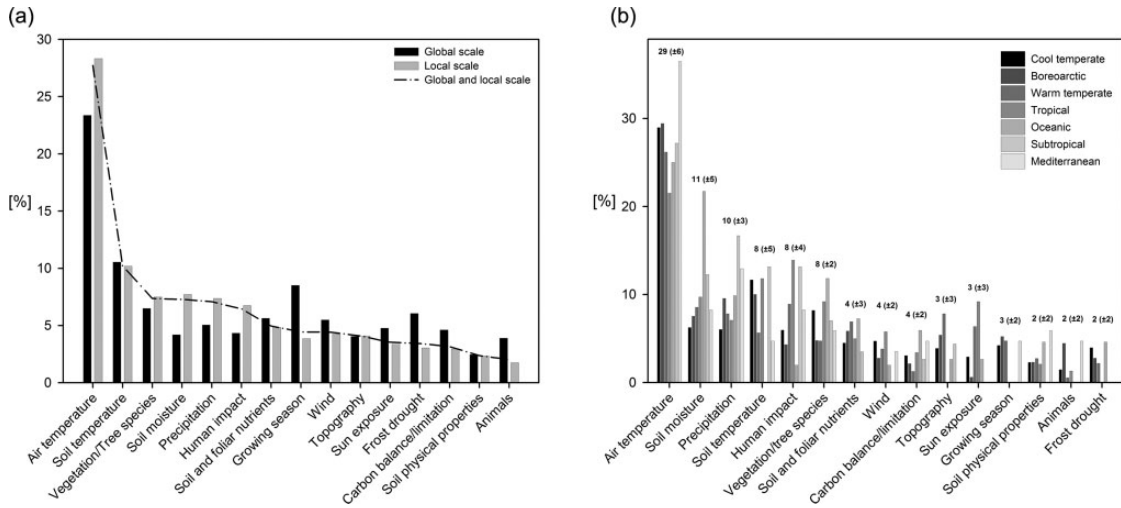
Figure 3. Relative importance (%) of factors controlling tree growth at its upper limit regarding (a) different spatial scales and (b) different ecozones. Studies including different spatial scales (miscellaneous) are excluded from (b). Mean $\pm$ standard deviation is given for each ecozone.

focus on soil related factors, as being the main subject of this study. Soil temperature was found to be the factor with the second highest relative importance for tree growth, both at a global and a local scale (Figure 3(a)). A main issue at this point might be that temperatures in general are easier to calculate and to evaluate at a global scale than other local factors (e.g. soil patterns, human impact). However, there is overwhelming evidence that temperature is the dominant control of treelines, which might also be a reason why temperature is mostly measured in literature. Soil moisture and water availability are among the most discussed factors, and are supposed to have the fourth highest relative importance for tree growth, however greater at a local than at a global scale (Figure 3(a)). Soil and foliar nutrients (especially N and P) are still underrepresented with a relative importance of 5% at a global and a local scale compared to soil temperature (10%) and soil moisture (7%; Figure 3(a)). This suggests that nutrients are less important for tree growth under extreme conditions. However, many recent findings not related to alpine treelines show the dominant

importance of soil nutrients, e.g. phosphorus (e.g. Bergh et al., 2014; Kanzler et al., 2015; Wang et al., 2011), and the results of our study might reflect the fact that scientific understanding is constantly evolving. This awareness also concerns other factors such as soil physical properties (including soil texture, soil organic matter quality, etc.) and carbon (C) balance/limitation, with relative importance below 5% (Figure 3(a)), respectively. For example, it is unlikely that the C balance/limitation has a minor effect on tree growth since C is a major nutrient. More research is necessary to better understand its importance for tree growth, which is supported by our data from Nepal (see next chapter), suggesting a possible C limitation. Further factors that influence acquiring and recycling of nutrients in soils, like mineral weathering, frost-thaw-cycling (permafrost-affected soils), soil microorganisms, and mycorrhizal fungi, are highly underrepresented in treeline literature. For that reason we excluded them from Figure 3(a) and (b).

Interestingly, we found major differences in the relevance of treeline-controlling factors for

tree growth in different ecozones (Figure 3(b)). Naturally, air temperature is expected to affect tree growth in all ecozones but is more distinct in seasonal climate regions like the Mediterranean with 37% relative importance than in tropical regions with high daily variance but almost no changes during the year and only 22% relative importance. Soil temperature seems to play a major role at tropical, subtropical, cool temperate and boreoarctic treelines, and has not been named as controlling factor at oceanic island treelines (Figure 3(b)). In contrast, soil moisture deficits and seasonal drought stress are assumed to be crucial in particular at oceanic, and semi-arid and arid subtropical treelines (Figure 3(b)). On oceanic islands (e.g. Tenerife), microclimate plays an important role. During the rainy season on such islands, mountains are covered by a permanent cloud belt reaching up to a certain altitude to which trees are growing, whereas the alpine belt above treeline is free from clouds due to steady winds restricting orographic lifting of clouds. This leads to semi-arid conditions with low rainfall, low soil moisture, and a high evaporative demand above the treeline (cf. Köhler et al., 2006). However, such results have to be considered with great caution because the number of publications from such study sites is still small compared to other ecozones (Figure 2). Again, the amount of studies dealing with soil and foliar nutrients, and especially with soil physical properties related to the total amount of publications is too small.

In general, the literature assessment clearly shows different results amongst many authors with regards to the relative importance of treeline-controlling factors. Independent from single factors, contrasts in valuation are often related to the scale type (Figure 3(a)) and the ecozones (Figure 3(b)) where the research was conducted. In addition, previous treeline literature may be dominated by a few researchers, which might face a bias problem. In our experience from the literature review and many discussions with treeline researchers, previous findings and conclusions are based on serious research results though, and are not speculative by nature. However, quantitative and experimental research is urgently needed.

Overall, our review indicates that, at a global scale, the majority of studies in current literature implicate growing season mean air and soil temperatures as the most important limiting factors for tree growth at its upper limit (Figure 3(a)). A similar pattern was found for the local scale (Figure 3(a)). These results may be even more strengthened by the fact that air and soil temperatures have possible direct effects on tree growth. Especially soil moisture, precipitation, and human impact are expected to play by far a more important role at the local scale compared to the global scale (Figure 3(a)), and vary greatly between the different ecozones (Figure 3(b)). In general, besides a potential direct limitation by temperature and moisture, all other factors are assumed to act as thermal modifiers, physiological stressors, or disturbance at different spatial scales, as shown in Table 1. This sort of hierarchy of factors should account for this type of thinking around treeline-controlling factors presented in the literature review.

2 Soil properties affecting tree growth at its upper limit

Although there is much literature on treelines, only few specific soil-related studies have been conducted (e.g. Dawes et al., 2015; Gruber et al., 2009a, 2009b; Liu and Luo, 2011; Seastedt and Adams, 2001; Schmid et al., 2009). Many studies focus on soil temperature ($n = 88$; e.g. Aulitzky, 1960; Green, 1983; Havranek, 1972; Körner, 1998a; Körner and Paulsen, 2004; Walter and Medina, 1969), whereas, related to the total amount of studies, only few authors also investigate treeline soil ($n = 28$) and foliar nutrient status (e.g. Köhler et al., 2006; Li et al., 2008; Liptzin and Seastedt, 2009; Liptzin et al., 2012; Loomis et al., 2006; McNown and Sullivan, 2013; Shiels and

Sanford, 2001; Weih and Karlsson, 2001). Potential soil types and pedogenic processes occurring in treeline ecotones are discussed in greater detail for example in Stöhr (2007) and Holtmeier (2009).

The tree vegetation itself influences pedogenesis and thus soil nutrient conditions by amount, coverage and quality of litter (Holtmeier, 2009; Holtmeier and Broll, 2007; Shiels and Sanford, 2001; Stöhr, 2007). Trees or tree stands control soil temperatures and soil moisture, root growth, nutrient uptake, mineralization and decomposition (Broll and Holtmeier, 1994; Holtmeier, 2009; Holtmeier and Broll, 2007; Stöhr, 2007). In turn, soil properties may affect vegetation by soil temperature, water supply, decomposition, and plant-available nutrient supply, while soil forming processes and also the effects of soils on vegetation depend partially on the altitudinal change of climatic conditions (Dirnböck et al., 2003; Holtmeier, 2009).

In this study, we counted the major soil-related factors soil temperature, soil moisture and soil nutrient supply in relation to response variables under investigation (see Appendix S2). We separated between the kind of response (positive, negative, both, or no effect) to identify controversies and uncertainties in literature. Responses of variables are negative in terms of unfavorable soil conditions (e.g. low soil temperatures, low soil water availability, insufficient nutrient supply). Positive responses of variables indicate positive effects of soil conditions (e.g. positive effects of tree symbiosis with mycorrhizal fungi or microbial communities). In some cases, negative and positive responses occurred (e.g. single tree species are affected by soil warming in different ways). Soil factors sometimes did not show an effect on response variables. All variables indicated a mostly negative response to soil temperature which reflects the results of relative importance (%) of soil temperatures controlling tree growth at its upper limit with regard to soil-related factors (Figures

3(a) and (b)). For example, tree growth was mainly found ($n = 32$) being negatively affected by low soil temperatures (Appendix S2), followed by insufficient soil nutrient supply ($n = 16$), and limitations in soil water availability ($n = 13$). Positive responses were for instance detected for seedling germination, which showed a higher uptake of N from soils due to warmer soil temperatures (e.g. by experimental soil warming). Symbiosis with mycorrhizal fungi or microbial communities was discovered ($n = 2$) to have a positive effect for tree growth of treeline trees (Appendix S2). The interaction of tree islands above the timberline and soils is controlled by the paramount influence of wind speed and wind direction, which lead to inhomogeneous patterns of soil nutrient and moisture conditions inside and outside of tree islands, and on luv- and leeward sides of tree islands, respectively. Thus, no clear response of tree islands to soil-related factors was found.

The greatest uncertainties exist for responses of tree growth, seedling performance, and photosynthesis, respectively, to soil temperature and soil moisture. Soil depth and soil texture are clearly underrepresented, even though soil depth is an essential parameter for water and nutrient storage and tree rooting, and soil texture is one of the main characteristics to govern plant growth.

a Soil temperature. Soil temperature is assumed to be the second most important factor affecting tree growth at its upper limit (Figure 3(a)). Our review revealed 88 studies with more detailed focus on the effects of soil temperatures on tree growth at its upper limit. Hereby, the main investigated response variables are tree growth, tree shoot and root growth, tree photosynthesis and respiration (growth limitation hypothesis), treeline position, and seedling abundance and establishment (Appendix S2).

Soil temperature regime and thresholds at alpine treelines are generally well documented, both at a global and a local scale. Throughout

diverse ecozones, soil temperature can be regarded as one of the fundamental soil properties that control tree growth (Figure 3(b)). Several authors (e.g. Dong et al., 2011; Körner, 1998a, 2012; Körner and Paulsen, 2004) state that growing season soil temperatures are among the most critical factors for the worldwide upper limit of tree growth. Many studies show low soil temperatures to affect tree growth by a reduction or an impediment of photosynthesis ($n = 6$, Appendix S2; e.g. Dong et al., 2011; Havranek, 1972; Stöhr, 2007), root respiration and root water uptake (Mayr, 2007; Walter, 1973; Walter and Medina, 1969), root growth ($n = 5$, Appendix S2; e.g. Alvarez-Uria and Körner, 2007; Stöhr, 2007), and radial growth (Dong et al., 2011). Likewise, low soil temperatures control decomposition, nutrient uptake, seed germination, seedling growth, maturing of annual shoots, or storage of reserves (Holtmeier, 2009; Körner, 2003b; Kullman, 2007; Stöhr, 2007; Tranquillini, 1979).

In general, cold soils with temperatures below 5°C impede biological activity and therefore nutrient supply (Holtmeier, 2009; Körner, 2012). In the European Alps, a temperature below 4°C (Tranquillini, 1979) was found to impede root growth and activity, but also to affect above-ground metabolism and growth. In the Giant Mountains, Czech Republic, cambial activity of *Picea abies* increased significantly at temperatures higher than 4–5°C (Treml et al., 2015). A critical soil temperature of 6°C for root growth is reported by Alavarez-Uria and Körner (2007) for the cool temperate treeline in the Swiss Alps. In New Zealand, Benecke and Havranek (1980) assessed restricted water uptake by trees below 5°C, and Havranek (1972) found net photosynthesis to be adversely affected and shoot growth to be limited lower than 7°C. Also, nutrient uptake and seedling growth were found to cease below this threshold at the boreoarctic treeline in Northern Sweden (Karlsson and Nordell, 1996; Karlsson and Weih, 2001). Similarly, *Picea engelmannii* and *Pinus contorta* in the Medicine Bow Mountains, USA,

growing in cold soils associated with snow pack, had 25–40% lower leaf photosynthesis than trees in warmer soils (Day et al., 1989). In the same study area, DeLucia (1986) found soil temperatures below 8°C to sharply reduce photosynthesis of *Picea engelmannii* seedlings.

A well-accepted temperature threshold for tree growth at alpine treelines is the mean soil temperature during growing season (Körner, 2012; Körner and Paulsen, 2004). Körner and Paulsen (2004) define the growing season as the period, when daily mean soil temperatures at 10 cm depth first exceed 3.2°C until they drop again below 3.2°C. However, growing season onset and end temperatures can exhibit small-scale variation, as shown by Gehrig-Fasel et al. (2007, 2008) in the Swiss Alps. At a global scale, a growing season mean soil temperature of 6.4 ± 0.7°C in 10 cm soil depth (cf. Table 2, Figure 4) was suggested as a threshold temperature under trees at treeline elevations (Körner, 2012). At a local scale, diverse additional and deviating data exist for a growing season mean soil temperature at alpine treelines, ranging from 5 to 12°C (Table 2). Most data arrives from measurements in 10 cm soil depth, however some authors report from data measured in 5 cm or deeper (15, 20, 30, 50 cm) or in differing time periods (e.g. Bendix and Rafiqpoor, 2001; Cierjacks et al., 2008; Greenwood et al., 2015; Hättenschwiler et al., 2002; Hertel and Wesche, 2008; Karlsson and Weih, 2001; Liu and Luo, 2011; Rossi et al., 2007; Sveinbjörnsson et al., 2010; Walter and Medina, 1969; Wininger, 1981), which are not included in Table 2.

A growing season mean soil temperature of 5.8°C in 10 cm depth was detected at a *Betula utilis* treeline in Langtang, Nepal, ca. 100 km west of Rolwaling (Körner, 2012). In contrast, in 2013 – a normal year with respect to meteorological events in the study area – we measured a growing season mean soil temperature of 7.6 ± 0.6°C at the Rolwaling treeline under uppermost forest stands of *Abies spectabilis* and *Betula utilis* (Table 2, Figure 4).

Table 2. Comparison of growing season mean soil temperatures (GSMT) at alpine treelines at 10 cm soil depth. The growing season is defined as the period, when daily mean soil temperatures at 10 cm depth first exceed 3.2°C until they drop again below 3.2°C (Körner and Paulsen, 2004). Some authors use different definitions for growing season: May–November (González de Andrés et al., 2015), June–August (Sullivan et al., 2015), May–September (Treml et al., 2015), December–April (Fajardo and Piper, 2014), December–February (Cieraad and McGlone, 2014), June–August (Loomis et al., 2006), May–November (Bernoulli and Körner, 1999).

Study area	Ecozone	GSMT (°C) at 10 cm depth	Reference
Worldwide (26 data sets)	–	6.4 ± 0.7	Körner (2012)
Worldwide (13 data sets)	–	6.6 ± 0.2	Hoch and Körner (2012)
Worldwide (ca. 50 data sets)	–	6.7 ± 0.8	Körner and Paulsen (2004)
Peru	Tropics, humid to semi-arid	4.6 – 5.1	Kessler et al. (2014)
Andes, Bolivia	Subtropics, arid	5.4 ± 0.1	Hoch and Körner (2005)
Mexico	Subtropics, humid	6.1 ± 0.7	Hoch and Körner (2003)
Rolwaling Himal, Nepal	Warm temperate, humid	7.6 ± 0.6	This study
Spanish Pyrenees	Warm temperate, humid to semi-arid	8.2 ± 0.2	González de Andrés et al. (2015)
Eastern Himalayas	Warm temperate, humid	6.6 ± 1.3	Shi et al. (2008)
Giant Mountains; Czech Rep.	Cool temperate, humid	6.9	Treml et al. (2015)
Southern Andes; Chile	Cool temperate, humid	6.6 ± 2.4	Fajardo and Piper (2014)
New Zealand	Cool temperate, humid	9.5 – 9.6	Cieraad and McGlone (2012)
Mount Brocken, Germany	Cool temperate, humid	6.7	Hertel and Schöling (2011)
Sygera Mountains, Tibet	Cool temperate, humid	8.0 ± 0.2	Liu et al. (2011)
Swiss Alps	Cool temperate, humid	6 – 7	Hoch and Körner (2009)
Swiss Alps	Cool temperate, humid	7.1 ± 0.5	Gehrig-Fasel et al. (2008)
Swiss Alps	Cool temperate, humid	7.0 ± 0.4	Gehrig-Fasel et al. (2008)
Swiss Jura	Cool temperate, humid	6	Körner and Hoch (2006)
Swiss Alps	Cool temperate, humid	6.7	Hoch and Körner (2003)
Swiss Alps	Cool temperate, humid	6.5	Hoch et al. (2002)
Swiss Alps	Cool temperate, humid	7.5	Bernoulli and Körner (1999)
Alaska	Boreoarctic, humid	4.9 ± 0.4	Sullivan et al. (2015)
Ural Mountains	Boreoarctic, humid	8.0 – 11.7	Hagedorn et al. (2014)
Alaska	Boreoarctic, humid	6	Loomis et al. (2006)
Northern Sweden	Boreoarctic, humid	6.5	Hoch and Körner (2003)

The northeast-exposed slope (NE) showed 0.2 to 0.4 K warmer soil temperatures compared to the northwest-exposed slope (NW), to be attributed to higher solar radiation on NE-exposed slopes. This is reflected by the length of growing season in 2013, which lasted 162 days on the NW-exposed slope compared to 177 days on the NE-exposed slope (means along transects, respectively). Hereby, the growing season length varied also greatly between different altitudinal zones (NW: A = 171, B = 175, C = 157, D = 145; NE: A = 178, B = 186, C = 164, D = 182). The length of growing season at treeline (transition zones B to C) in 2013 was on average 20-30 days longer than pretended 140–150 days for warm-temperate treelines (Körner, 2012). Considerably higher threshold soil temperatures in Rolwaling indicate significant local deviations from global mean values and suggest reservation when attempting at global generalizations of local patterns. Using the growing season mean soil temperature of 6.4 ± 0.7°C (Körner, 2012) as a predictor for
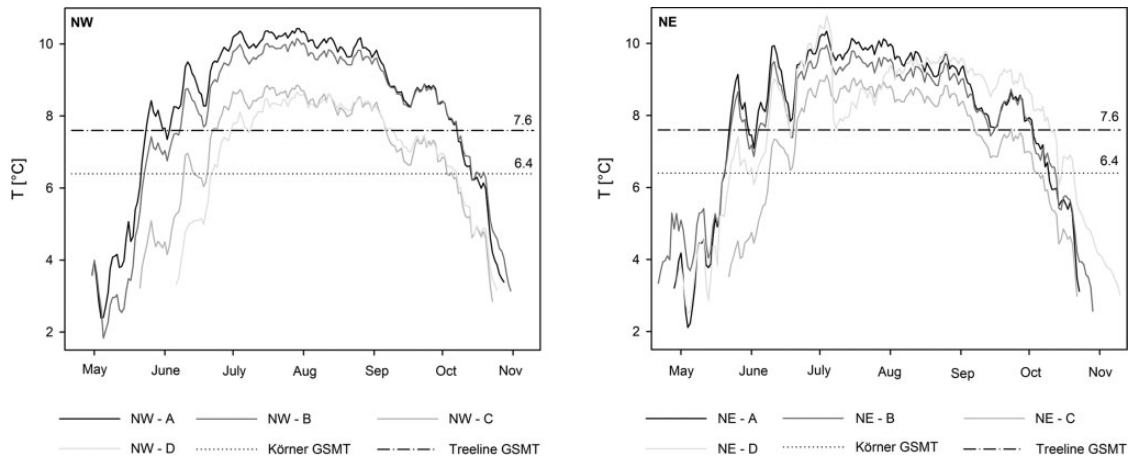
Figure 4. Daily mean soil temperatures of altitudinal zones A (closed forest), B (closed forest), C (krummholz zone) and D (dwarf shrub heath) on a NE- and a NW-exposed slope and growing season mean soil temperature (GSMT, 7.6°C, 10 cm depth) at treeline (transition zones B to C) in Rolwaling Himal, Nepal, in relation to the 6.4°C threshold temperature for tree growth (Körner, 2012) during growing season. For start and end of growing season we used the soil temperature threshold of 3.2°C defined by Körner and Paulsen (2004).

treeline position, the treeline in Rolwaling would be located 500–600 m higher in elevation. This result makes us question the paramount role of soil temperature since it indicates that such a distinct higher temperature does not necessarily correspond with treeline shift. Currently, the treeline position is rather stable, and a considerable treeline advance is not to be expected in the medium-term (several years to a few decades; Schickhoff et al., 2015).

Table 2 indicates both latitude- and local scale-dependent variations in growing season mean soil temperatures at alpine treelines, suggesting that it makes sense to differentiate between tropical and extratropical (subtropical, cool/warm temperate, boreoarctic, Mediterranean), and oceanic treelines, respectively. Tropical treelines experience nearly consistent soil temperatures all year round, whereas extratropical treelines are characterized by seasonal variations. Especially, treeline growing season mean soil temperatures in the tropics (e.g. Peru), subtropics (e.g. Bolivia), and at warm temperate treelines (e.g. Rolwaling, Spain) differ from

Körner's paradigm (cf. Table 2, respectively). However, widely differing soil temperatures are also reported from cool temperate treelines (e.g. New Zealand). Thus, we do not support the general validity of certain soil threshold temperatures for all treeline environments without a broader error term than ± 0.7°C, and underline significant local deviations. Referring to the results of the literature review (Figure 3(b)), soil temperature is assumed to be of great relevance for tree growth at cool temperate, boreoarctic, tropical and subtropical treelines, whereas other factors (e.g. soil moisture) are considered more important than soil temperature at warm temperate, oceanic and Mediterranean treelines.

Lower mean growing season soil temperatures under closed forest compared to soil temperatures above treeline is a common pattern observed along altitudinal transects in different ecozones, where dense tree canopies prevent soil heat flux and radiative warming of their own rooting zone (e.g. Bader et al., 2007; Bendix and Rafiqpoor, 2001; Gruber et al., 2009b; Holtmeier and Broll, 2010; Kessler and

Hohnwald, 1998; Oberhuber, 2007; Wieser and Tausz, 2007). It has been shown that small-stature plants above treeline are decoupled from free atmosphere and profit from soil warming and an associated microclimate with a positive solar radiation balance and therefore a higher tissue temperature (e.g. Aulitzky, 1961; Doležal and Šrutek, 2002; Germino et al., 2002; Holtmeier, 2009; Körner, 1998a, 2012). According to Holtmeier (2009), this results in enhanced survival rates and reproduction when sufficient water and nutrients are provided. Our soil temperature monitoring across the Rolwaling treeline ecotone does not completely support the findings of higher soil temperatures above treeline (Figure 4). In general, we found a clear altitudinal gradient of generally decreasing both annual mean and growing season mean soil temperatures from closed forest (zones A, B) to krummholz zone (C) and dwarf shrub heath (D). A variance analysis (Kruskal–Wallis) with subsequent post-hoc Nemenyi test revealed major differences ($p < 0.0001$) in daily mean soil temperatures during growing season between AB ($p = 0.73$) and CD ($p = 0.90$). On the NW-exposed slope, same tests resulted in significantly similar daily mean soil temperatures in A and B ($p = 0.92$), and C and D ($p = 0.86$). The NW-exposed slope shows a clearly altitudinal soil temperature gradient during all seasons. However, temperatures were similar in krummholz (NW-C) and under dwarf shrubs (NW-D) from August to October 2013 (Figure 4). The effect of dense tree canopies preventing soil heat flux and radiative warming on soil temperatures was observed during certain time periods in the entire year, however on the NE-exposed slope only (similar temperatures in A and B ($p = 0.41$), and A and D ($p = 0.87$)), but did not dominate the overall altitudinal gradient with a strong decline in soil temperatures at transition from B to C (treeline). Hereby, soil temperature was higher under dwarf shrubs (NE-D) compared to the krummholz zone (NE-C) all year

except for July 2013 (Figure 4), and higher compared to the closed forest (NE-A, NE-B) on a few days in May 2013, end of July/beginning of June 2013, and from August to beginning of November 2013 (Figure 4).

b Soil moisture. From 507 investigated studies, merely 33 studies concentrate on the relation between soil moisture and tree growth in more detail. Hereby, the main response variables are tree growth, treeline position, seedling establishment, and seed germination (cf. Appendix S2). More studies are needed especially from subtropical, Mediterranean, and oceanic treelines, to clarify the role of soil water availability for tree growth at its upper limit. Further, more information especially with regards to soil moisture monitoring in higher spatial and temporal resolution is necessary, as for example conducted by Biondi et al. (2005) and Biondi and Hartsough (2010) at the tropical treeline in Mexico, and by McNown and Sullivan (2013) at the boreoarctic treeline in Alaska.

Despite a low number of publications, soil moisture has been named as one of the most important soil properties to control tree growth in treeline ecotones: It is listed fourth in relative importance for tree growth (Figure 3(a)). With regard to ecozones (Figure 3(b)) soil moisture is expected being more important in semi-arid/arid subtropical, and oceanic island regions compared to boreoarctic, cool and warm temperate, or tropical regions. Accordingly, the role of soil moisture for tree growth in treeline ecotones is co-controlled by climate especially by global circulation patterns like monsoon and ENSO. However, Körner (2012) assumes soil moisture not to affect tree growth at a global scale, which is in line with findings at a local scale (e.g. Neuwinger-Raschendorfer, 1963; Shrestha et al.; 2007; Slatyer, 1976).

However, at a local scale, soil moisture conditions and water availability can be highly variable due to small-scale mosaics of (micro-) topography (Ferrar et al., 1988), (micro-)
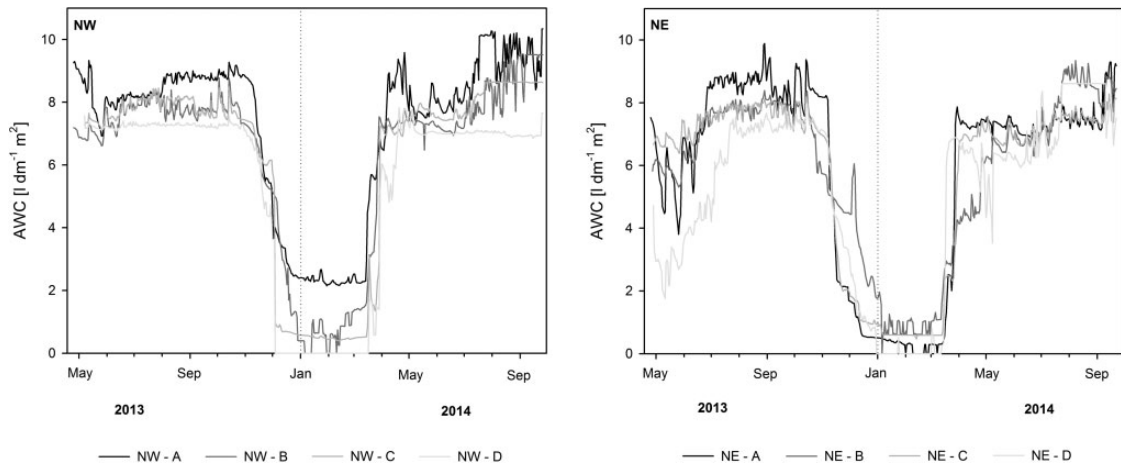
Figure 5. Spatial and temporal variation in available water capacity (AWC; L dm^{-1} m^{-2}) in altitudinal zones A (closed forest), B (closed forest), C (krummholz zone) and D (dwarf shrub heath) on a NE- and a NW-exposed slope in Rolwaling.

climate, vegetation cover, and due to micro-scale variation in soil depth, type and structure (Broll et al., 2007; Wieser et al., 2009). For example, humus-rich upper horizons of forest soils had higher water-holding capacities and showed highest soil moisture compared to stony, coarse grained soils above the treeline in Colorado, USA (Wardle, 1968). Further, variation in snow pack and the onset of snowmelt rule soil water availability in treeline ecotones, and thus are assumed to be an important factor for tree growth and seedling establishment at a local scale (e.g. Barbeito et al., 2012; Batllori and Gutiérrez, 2008; Daniels and Veblen, 2004; Holtmeier, 2009; Holtmeier and Broll, 2007; Peterson, 1998; Richardson and Friedland, 2009; Shrestha et al., 2007; Wilmking et al., 2006).

Low soil water availability during different time periods of the year was found to affect tree growth and seedling establishment in all eco-zones (Ferrar et al., 1988; Gaire et al., 2014; Liang et al., 2014; Öberg and Kullman, 2012), and particularly in arid and semi-arid subtropical or oceanic island treeline ecotones (cf. Figure 3(b); Fajardo et al., 2011; Gieger and Leuschner, 2004; Köhler et al., 2005; Lara et al., 2005; Leuschner and Schulte, 1991; Morales et al.,

2004). In contrast, high soil water contents were found to negatively affect tree growth at tropical treelines in Ecuador and Peru (Peters et al., 2014).

In Rowaling, we calculated spatial and temporal variation in soil available water capacity (AWC; L dm^{-1} m^{-2}; Figure 5). Hourly year-round measurements show soil available water capacities between 6 and 10 L dm^{-1} m^{-2} during summer (June–September) and beginning of autumn (October). During autumn (November), soil available water capacities dramatically drop to very low values of 0 to 2 L dm^{-1} m^{-2} until April (Figure 5), which indicates a significant constraint in soil water supply during pre-monsoon months (March, April). This is in accordance with a reduced abundance of tree seedlings and saplings of *Abies spectabilis*, *Betula utilis*, *Rhododendron campanulatum*, and *Sorbus microphylla* (Schickhoff et al., 2015). We also found positive correlations between soil nutrients (N, C, N, Na, K, Mg, Ca, Mn, Fe, Al) and soil moisture, however not significant. Other variables may control seedling abundance as well. Soils across the treeline ecotone in Rolwaling were frozen from end of October at least until end of April. In combination with a very low precipitation from

November to May, this results in very low available water capacities in soils. We found evergreen tree saplings and dwarf shrubs growing above treeline to be likely affected by frost drought (also described by Larcher, 1957, 1963; Kupfer and Cairns, 1996; Mayr et al., 2003, 2006a, 2006b, 2014), showing yellowish and brownish leaves and their deformation (rolling).

Our results do not only question a common understanding that alpine treelines are not affected by soil moisture (e.g. Körner, 2012) but help to understand how soil water availability can limit tree recruitment and encourage further research on the mechanisms of seedling and sapling establishment across alpine treelines.

c Soil nutrients. A considerable number of studies (e.g. Birmann and Körner, 2009; Fajardo et al., 2012, 2013; Karlsson and Nordell, 1996; Körner, 1989; Macek et al., 2012; Sveinbjörnsson, 2000) focus on nutrient uptake and investment by plants within alpine treeline ecotones, whereas only a few concentrate on nutrient status and availability in soils (Köhler et al., 2006; Liptzin et al., 2012; Loomis et al., 2006; McNown and Sullivan, 2013; Sullivan et al., 2015; Thébault et al., 2014; Weih and Karlsson, 2001; Zhang et al., 2011). Quantitative and experimental studies focusing on soil nutrients are rare, and tree physiological experiments for treeline species are missing. Our review exposed merely 28 studies with focus on soil nutrients (mainly N, Nmin, P, C). The main response variable is tree growth (cf. Appendix S2). The majority of studies dealing with nutrient status in treeline ecotones examine foliar nutrients, and hereby especially whether tree growth is C limited or not (carbon sink/source limitation hypothesis; e.g. Körner, 1998a). Soil and foliar nutrients are expected to be of moderate importance for tree growth, both at a global and a local scale (Figure 3(a)). Concerning specific ecozones, soil and foliar nutrients also seem to be of moderate relevance at cool

temperate, boreoarctic, warm temperate, tropical, subtropical, and oceanic treelines, but are unlikely to affect tree growth at Mediterranean treelines (Figure 3(b)). These conclusions mainly arrive from their limited literature reviews.

N is considered as the most limiting nutrient to primary production in terrestrial plants (Vitousek and Howarth, 1991) including treeline trees (Haselwandter, 2007). Accordingly, reduced soil N availability could affect tree growth performance at treelines. However, several studies in different ecozones found even higher concentrations of N and C, such as sugars, starch, and lipids, in soils and trees at treeline compared to lower altitudes (Bansal and Germino 2008; Fajardo et al., 2012, 2013; Hertel and Wesche, 2008; Hoch and Körner, 2003; Hoch et al., 2002; Körner, 1989, 1998b, 2003b, 2012; Liptzin et al., 2012; Shi et al., 2008; Weih and Karlsson, 2001). These findings were interpreted as evidence that treelines are rather a nutrient sink than a nutrient source, and that treeline trees are C sink limited (e.g. Körner, 1998a; Seastedt et al., 2004; Smith et al., 2003). Following this, C as a soil nutrient is thought not to be directly relevant to treeline tree growth. Trees are assumed to not being able to use obviously sufficient nutrients for growth as a result of low soil temperatures. For example, Weih and Karlsson (2001) found increasing foliar N at cooler temperatures to result from weaker N dilution by reduced growth, and therefore to reflect a physiological adaptation to low temperatures. In a study on Niwot Ridge, Colorado, total soil C, total soil and available N, and total soil and available P, as well as exchangeable cations were found to be gradually higher in the krummholz zone and tundra compared to the closed forest below (Liptzin et al., 2012). Similarly, increasing soil N with elevation was found in a warm temperate treeline ecotone in central Nepal (Shrestha et al., 2007). Further, Zimmermann et al. (2010) detected higher soil N under tundra compared

to forest at the tropical treeline in Peru. Consequently, Körner (1989, 2012) and Körner and Hoch (2006) see no indication of a nutrient shortage at alpine treelines. In this context, symbiosis with ectomycorrhizal fungi is assumed to be important for trees to reach their upper limit (Haselwandter, 2007; Körner, 2012) because mycorrhizae withstand cooler temperatures than trees do (Körner, 2012). The most abundant tree species and basidiomycota in temperate treeline ecotones are reviewed in Haselwandter (2007).

However, several studies from cool temperate, warm temperate, boreoarctic, tropical, subtropical, and oceanic treelines (cf. Figure 3(b)) assessed lower N cycling rates (e.g. nitrification and denitrification) and contents in treeline soils compared to soils at lower altitudes (Frangi et al., 2005; Huber et al., 2007; Loomis et al., 2006; McNown and Sullivan, 2013; Shi et al., 2006; Sullivan et al., 2015; Sveinbjörnsson, 2000; Thébault et al., 2014; Wittich et al., 2012), as well as lower tissue N contents in treeline trees (Garkoti and Singh, 1992, 1994; Gieger and Leuschner, 2004; Huber et al., 2007; Köhler et al., 2006; McNown and Sullivan, 2013; Richardson, 2004; Shi et al., 2006; Sullivan et al., 2015; Sveinbjörnsson, 2000; Wittich et al., 2012). For example, soil N mineralization was found to decrease fivefold from contiguous forest stands to the krummholz zone in a boreoarctic treeline ecotone in Alaska (Loomis et al., 2006; Sveinbjörnsson, 2000). Also, Huber et al. (2007) report a significant decrease of soil N with elevation at the temperate treeline of Mt. Schrankogel, Austria. Köhler et al. (2006) found low soil N concentrations along an altitudinal transect in the oceanic treeline ecotone of Mt. Teide, Tenerife, compared to more humid treeline environments. For tropical montane forests in Ecuador nutrient deficiency has been suggested to reduce tree growth along an altitudinal transect caused by reduced organic matter turnover at higher altitudes (Soethe et al., 2008; Wilcke et al., 2008). These altitudinal gradients mainly result from cold soil temperatures and
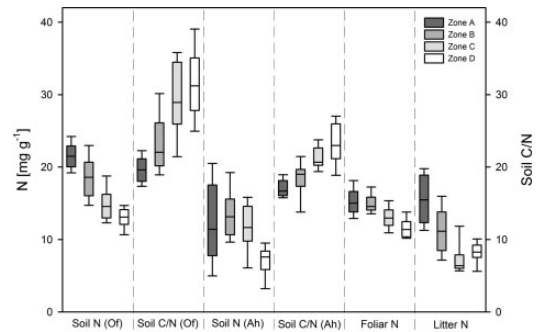
Figure 6. Nitrogen (N) concentrations [mg g^{-1}] in soils (Of layer, Ah horizons), foliage (*Rhododendron campanulatum*) and litter, and soil C/N ratio (Of, Ah) in altitudinal zones A (closed forest), B (uppermost closed forest), C (krummholz) and D (dwarf shrub heath) on NE- and NW-exposed slopes in Rolwaling Himal.

poor soil quality which lead to slower rates of potential soil respiration, reduced photosynthesis, hampered litter decomposition and soil N mineralization, and constrained growth of treeline trees (Huber et al., 2007; Loomis et al., 2006; McNown and Sullivan, 2013; Sveinbjörnsson, 2000). Another explanation for a constrained tree growth at its upper limit is competition of trees with microorganisms for limited soil nutrients (N, C). For N, this is reported from a treeline ecotone on the Tibetan Plateau (Liu et al., 2012). Similarly, tree growth in a cool temperate treeline ecotone in Patagonia is expected to be limited due to competition between trees and soil microbial communities for decreasing soil inorganic N with elevation (Thébault et al., 2014).

In line with these findings, our own results from Rolwaling indicate a significant decline in soil, litter and foliar (species *Rhododendron campanulatum*) concentrations of N (Figure 6), K and Mg with elevation (Table 3). K and Mg also decrease in soil Ah horizons, however not significantly (Table 3). In foliage, similar results were found for tree species *Abies spectabilis* and *Sorbus microphylla* (not illustrated) which both occur in the closed forest and sparsely as krummholz above treeline, however here not in tree form as defined by Körner

Table 3. Selected nutrients in litter, soil and foliage in relation to elevation [m a.s.l.] (r = Spearman rank correlation coefficient, p = p-value), and pairwise comparison of nutrient concentrations between altitudinal zones A–D (χ^2 = Kruskal Wallis chi-squared; p = p-value; A, B, C, D = altitudinal zones). Significance level is $\alpha = 0.01$.

Nutrient	Sample material	Spearman correlation		Kruskal–Wallis		Post-hoc Nemenyi (Tukey)					
		r	p	χ^2	p	AB (p)	AC (p)	AD (p)	BC (p)	BD (p)	CD (p)
N	Litter layer	−0.65	<0.01*	77.51	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	0.35
	Of layer	−0.83	<0.01*	98.09	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	0.11
	Ah	−0.40	<0.01*	17.24	<0.01*	0.76	0.99	<0.01*	0.83	<0.01*	<0.01*
	Foliage	−0.67	<0.01*	47.18	<0.01*	0.99	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*
C	Litter layer	0.50	<0.01*	48.25	<0.01*	<0.01*	0.07	<0.01*	0.51	<0.01*	<0.01*
	Of layer	−0.19	0.02	19.22	0.07	0.35	0.60	0.09	0.98	0.03	0.02
	Ah	−0.13	0.36	10.13	0.02	0.59	0.41	0.49	0.99	0.05	0.02
	Foliage	0.28	0.02	5.74	0.13	0.99	0.34	0.25	0.42	0.32	0.99
C/N	Litter layer	0.66	<0.01*	78.51	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	0.47
	Of layer	0.77	<0.01*	87.04	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	0.53
	Ah	0.81	<0.01*	34.32	<0.01*	0.34	<0.01*	<0.01*	<0.01*	<0.01*	0.80
	Foliage	0.70	<0.01*	33.88	<0.01*	0.99	<0.01*	<0.01*	<0.01*	<0.01*	0.10
K	Litter layer	−0.72	<0.01*	93.67	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*	0.53
	Of layer	−0.41	<0.01*	27.54	<0.01*	0.99	<0.01*	<0.01*	<0.01*	<0.01*	0.57
	Ah	−0.09	0.54	1.09	0.79	0.97	0.96	0.98	0.79	0.86	0.99
	Foliage	−0.51	<0.01*	14.53	<0.01*	0.99	<0.01*	<0.01*	<0.01*	<0.01*	0.96
Mg	Litter layer	−0.73	<0.01*	83.07	<0.01*	0.53	<0.01*	<0.01*	<0.01*	<0.01*	<0.01*
	Of layer	−0.51	<0.01*	40.63	<0.01*	0.35	0.07	0.83	<0.01*	<0.01*	<0.01*
	Ah	−0.16	0.27	4.18	0.24	0.99	0.96	0.43	0.95	0.45	0.21
	Foliage	-0.44	<0.01*	14.24	<0.01*	0.89	0.97	<0.01*	0.59	<0.01*	<0.01*

*Highly significant at a significance level of $\alpha = 0.01$.

18

(2012) (>3 m height). Tree species *Betula utilis* and *Acer caudatum* (not illustrated) also indicate significantly decreasing foliar nutrient concentrations with elevation; however, they do not occur above treeline. This leads to new findings, that nutrient availability (N, K, Mg) decreases in soils and foliage with elevation not only for a single nutrient but generally, and, with regards to higher soil temperatures in Rolwaling compared to global mean values, might explain why treeline shift and global warming are decoupled.

Soil C concentrations (Of, Ah) slightly decrease with elevation, however not significantly (see also Speed et al., 2015; Zimmermann et al., 2010), whereas soil N concentrations (Of, Ah) significantly decrease (Figure 6). Thus, significantly increasing C/N ratios (Figure 6, Table 3; cf. e.g. Hertel and Wesche, 2008; Thébault et al., 2014) and significantly decreasing N in soils with elevation indicate decreasing soil nitrogen availability. This is confirmed by decreasing Nmin values with elevation (not illustrated).

Significantly decreasing C in litter, not significantly decreasing C in soil (Of, Ah), and not significantly increasing C in foliage (*Rhododendron campanulatum*, Table 3) with elevation (m a.s.l.) respectively, may indicate, along with a strong limitation in nutrients N, K, and Mg, a combination of C source and sink limitation (according to the C limitation hypothesis from Körner, 1998a) in the Rolwaling treeline ecotone. This assumption is strengthened by C concentration patterns in different altitudinal zones: besides litter C, we could not detect major differences between zones in foliar C and soil C (Of, Ah) (Table 3). Since leaching of organic acids and organomineral compounds is part of the podzolization process as a whole, C limitation might be a typical factor for treeline ecotones on podzols and other podzolic soils. This would also explain why we did not find a significant altitudinal gradient because podzolization is the main process of soil formation along the

entire slope, independent from the rate of C input from the vegetation. However, further investigations are necessary to understand this complex relationship more clearly. In general, more research is needed to better comprehend the role of nutrition for tree establishment and tree growth under such extreme environmental conditions.

IV Conclusions

In this paper, we review the state of the art on how soil properties affect tree growth at its upper limit in a global perspective. We specifically discuss those results in relation to ecozones and the scale-dependent importance of single factors, as well as in relation to new findings from Rolwaling Himal. Further, we identify existing gaps in the treeline literature and showed where new research is needed, both conceptual and geographical.

Our results show:

1. The approach of quantifying previous knowledge on treeline-controlling factors is the first of its kind. We show that soil properties have not received adequate attention in treeline research, and (in combination with our own findings from Rolwaling) that the role of major soil nutrients and soil moisture for treeline shift has been underestimated by far. This leads to new findings, e.g. that nutrient availability (N, K, Mg) decreases in soils and foliage with elevation not only for a single nutrient but generally, and might explain why treeline shift and global warming are decoupled. We also show that soil moisture deficit early in the year impedes seedling and sapling establishment, thus indicating an important mechanism to control the position of the treeline. This does not only question previous findings that alpine treelines are not affected by

soil moisture but helps to understand how soil water availability can limit tree recruitment and encourage further research on the mechanisms of seedling and sapling establishment across alpine treelines.

2. Further information especially with regard to soil moisture monitoring in higher spatial and temporal resolution is necessary. To clarify the role of soil water availability for tree growth at its upper limit, more studies are needed especially from subtropical, Mediterranean, and oceanic treelines.

3. Quantitative and experimental studies focusing on soil nutrients are rare, and tree physiological experiments for treeline species are missing. More research is needed to better understand the role of nutrition for tree establishment and tree growth under such extreme environmental conditions. The results from Rolwaling indicate that low soil nutrient availability is most likely affecting tree growth at its upper limit.

4. Our result of 7.6 $\pm$ 0.6°C for growing season mean soil temperature at treeline in Rolwaling is 1.2 K higher compared to the postulated 6.4 $\pm$ 0.7°C for alpine treelines. We suggest a broadening of the ± 0.7°C error term to cover the wide range at a local scale. Treelines with higher growing season soil temperatures will lag behind global warming in their position by considerably longer time periods than other treelines. We suggest long-term monitoring studies at near-natural treelines in different treeline environments as an efficient tool to analyze complex treeline dynamics.

5. Tree growth at the Rolwaling treeline may further be constrained by a combination of C source and sink limitation. Since leaching of organic acids and organomineral compounds is part of the podzolization process as a whole, C limitation might be a typical factor for treeline ecotones on Podzols and other podzolic soils. More research is needed to clarify these complex relations, also with regard to the shown low soil nutrient availability.

6. We suggest specific combinations of soil properties as well as single soil properties (low soil nutrient availability, limited soil water supply) may limit tree growth even below climatic treelines.

Declaration of Conflicting Interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Supplemental material

The online appendices are available at http://ppg.sagepub.com/supplemental.

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