Interactions among soil properties and variations in stand structures in the Rolwaling alpine treeline ecotone, Nepal

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List of Abbreviations

ATP	adenosine triphosphate
AWC	available water capacity
dbh	diameter at breast height
DJF	December, January, February
ENSO	El Niño and Southern Oscillation
HCl	hydrochloric acid
HNO_3	nitric acid
H_2O	water
H_2O_2	hydrogen peroxide
H_2SO_4	sulphuric acid
JJAS	June, July, August, September
KCl	potassium chloride
LAI	leaf area index
M	molar
MAM	March, April, May
m a.s.l.	meters above sea level
MLR	Multiple Linear Regression Analysis
MMR	Multivariate Multiple Linear Regression Analysis
m ü. NN	Meter über Normalnull
NADPH	nicotinamide adenine dinucleotide phosphate
NaOH	sodium hydroxide
$NaHCO_3$	sodium bicarbonate
NE	Northeast
NE1	Altitudinal transect Northeast 1
NE2	Altitudinal transect Northeast 2
NO_3^-	nitrate
NH_4^+	ammonium
NW	Northwest
NW1	Altitudinal transect Northwest 1
ON	October, November
PCA	Principal Component Analysis
RDA	Redundancy Analysis
Rhc	*Rhododendron campanulatum*
Rhas	*Rhododendron anthopogon* and *Rhododendron setosum*
SM	soil moisture
ST	soil temperature

1 Summary

In alpine treeline ecotones, little is known about how soil properties control tree growth and how soil properties interact with variations in stand structures and tree physiognomy. In particular, the effects of soil moisture variability on alpine treeline performance have not received adequate attention yet. Soil temperature patterns are generally well documented and soil temperature is considered a key factor in limiting tree growth at both global and local scales. Other than that, the interactions among the availability of soil nutrients and tree growth in treeline ecotones are barely explored. To fill these gaps, a multiple data sampling was performed in a near-natural treeline ecotone in Rolwaling Himal, Nepal.

This thesis (i) reviews the state of knowledge on soil properties at alpine treelines, and discusses the results specifically related to ecozones and to the scale-dependent importance of single factors; (ii) identifies gaps in literature and shows where new research is needed, both conceptual and geographical; (iii) in its main part investigates local scale effects of soil properties (temperature, moisture, nutrient availability, among others) on tree growth limitation, and their interactions with other abiotic and biotic factors in Rolwaling; (iv) contributes important findings in the framework of the "TREELINE" project to comprehend the sensitivity and response of the Rolwaling treeline ecotone to recent climate change.

The results show that at a global scale and throughout diverse ecozones, the mean soil temperature during growing season is crucial for tree growth. At the treeline in Rolwaling, a growing season mean soil temperature of 7.5 ± 0.6°C was measured, which is 1.1 Kelvin higher compared to the postulated 6.4 ± 0.7°C for alpine treelines at a global scale. A broadening of the ± 0.7°C error term is suggested to cover the wide range at a local scale. In Rolwaling, multivariate statistical analyses yield a significant relationship between soil temperatures and variations in stand structures and tree physiognomy (tree height, crown length, crown width, leaf area index). Vice versa, soil temperature variability is controlled by the stand structures themselves.

The effects of soil moisture on treeline performance have been insufficiently explored. A comprehensive long-time monitoring of soil moisture is extremely rare, and more studies are needed especially from subtropical, Mediterranean, and oceanic treelines. In Rolwaling, soil moisture conditions indeed appear to be less substantial for the current stand structures and tree physiognomy. Though, stand structures control soil moisture, which additionally is affected by snow cover. However, generally shallow and coarse-grained soils cause low water-holding capacities, and thus a remarkable amount of water percolates from the topsoils to the subsoils. In the alpine tundra with a missing forest canopy, year-round lowest available water capacities compared to the subalpine forest and krummholz below occur which are additionally caused by high solar radiation, wind, and thus high evaporation. This may impede seedling and sapling establishment especially in this area, which could be an important mechanism that controls treeline position.

Furthermore, the interactions among major soil nutrients (esp. nitrogen, phosphorus) and tree growth in alpine treeline ecotones have been underrated considerably at all scales. In Rolwaling, analyses of the soil and foliar carbon:nitrogen:phosphorus (C:N:P) stoichiometric ratios, and plant-available N and P in soils indicate a general limitation in N and P, which is significantly increasing with elevation [m a.s.l.] and with altitudinal changes in stand structures. This holds true for other nutrients (e.g. potassium, magnesium) in both soils and foliage. Nutrient deficiency may explain why potential treeline shift and global warming are decoupled (higher soil temperatures at the Rolwaling treeline than the global mean).

In summary, this thesis questions previous results arguing that alpine treelines are unaffected by soil nutrient and moisture availability. In Rolwaling, specific combinations of soil properties as well as single soil properties may limit tree growth even below climatic treelines.

2 Zusammenfassung

In Waldgrenzökotonen ist wenig darüber bekannt, wie Bodeneigenschaften Baumwachstum beeinflussen und mit Veränderungen in der Bestandsstruktur und der Physiognomie von Bäumen interagieren. Besonders die möglichen Auswirkungen der Variabilität von Bodenfeuchte auf das Verhalten von alpinen Baumgrenzen haben bisher keine ausreichende Aufmerksamkeit erhalten. Die Bodentemperaturverhältnisse in Waldgrenzökotonen sind insgesamt gut dokumentiert und werden als ein Hauptfaktor für die Limitierung von Baumwachstum angesehen, sowohl auf globaler wie auch auf lokaler Ebene. Die Wechselwirkungen zwischen verfügbaren Bodennährstoffen und Baumwachstum in Waldgrenzökotonen wurden dagegen bisher kaum erforscht. Um diese Forschungslücken zu schließen, wurden wiederholt Messungen und Beprobungen in einem naturnahen Waldgrenzökoton im Rolwaling Himal (Nepal) vorgenommen.

Die vorliegende Arbeit (i) prüft den aktuellen Wissensstand über Bodeneigenschaften an alpinen Baumgrenzen und diskutiert die Ergebnisse bezogen auf Ökozonen und auf die maßstabsabhängige Bedeutung einzelner Faktoren; (ii) deckt Lücken in der Literatur auf und zeigt, wo neue Forschung notwendig ist, sowohl in konzeptioneller als auch in geografischer Hinsicht; (iii) untersucht in ihrem Schwerpunkt die Auswirkungen von lokalen Bodeneigenschaften (Temperatur, Feuchte, Nährstoffverfügbarkeit, u.a.) auf eine mögliche Limitierung von Baumwachstum im Rolwaling und deren Wechselwirkungen mit anderen abiotischen und biotischen Faktoren; (iv) liefert einen wichtigen Beitrag zum “TREELINE”-Forschungsprojekt, um die Sensitivität und Reaktion des Waldgrenzökotons im Rolwaling auf den jüngsten Klimawandel zu verstehen.

Die Ergebnisse zeigen, dass auf globaler Ebene und in verschiedenen Ökozonen die Durchschnittstemperatur im Boden während der Vegetationsperiode entscheidend für Baumwachstum ist. An der Baumgrenze im Rolwaling wurde in dieser Zeit eine mittlere Bodentemperatur von 7.5 ± 0.6°C gemessen, die um 1.1 Kelvin höher ist im Vergleich zu den postulierten 6.4 ± 0.7°C an alpinen Baumgrenzen in globaler Perspektive. Es wird eine Vergrößerung der Standardabweichung von ± 0.7°C vorgeschlagen, um die große Spanne auf

lokaler Ebene zu decken. Im Untersuchungsgebiet haben multivariate statistische Analysen signifikante Zusammenhänge zwischen Bodentemperaturen und den Veränderungen in der Bestandsstruktur bzw. in der Physiognomie von Bäumen ergeben (Baumhöhe, Kronendurchmesser, Kronenradius, Blattflächenindex). Im Gegenzug werden Veränderungen in den Bodentemperaturen durch die Bestandsstruktur selbst gesteuert.

Die Auswirkungen von Bodenfeuchte auf Baumwachstum an alpinen Baumgrenzen sind bis heute zu wenig erforscht. Flächendeckende Langzeitmessungen der Bodenfeuchte sind äußerst selten und fehlen vor allem an subtropischen, mediterranen und ozeanischen Baumgrenzen. Statistische Analysen zeigen, dass die Bodenfeuchtebedingungen im Rolwaling für die rezente Bestandsstruktur und Physiognomie der Bäume in der Tat weniger von Bedeutung zu sein scheinen. Im Gegenzug steuern Letztere die Bodenfeuchtebedingungen, die zusätzlich von der Schneedecke beeinflusst werden. Im gesamten Untersuchungsgebiet jedoch führen flachgründige und grobkörnige Böden zu allgemein geringen Wasserhaltekapazitäten und eine große Menge Wasser versickert aus den Oberböden in die Unterböden. Ohne ein schützendes Blätterdach treten in der alpinen Tundra ganzjährig die niedrigsten nutzbaren Feldkapazitäten im Vergleich zu subalpinem Wald und Krummholz auf, die hier zusätzlich aus einem höheren Einfluss von Sonneneinstrahlung, Wind und somit höherer Verdunstung resultieren. Vor allem in diesem Bereich wird eine Etablierung von Sämlingen und Setzlingen erschwert - ein wichtiger Mechanismus, der die Position der Baumgrenze steuert.

Ebenso werden die Wechselwirkungen zwischen den Hauptnährstoffen in Böden (v.a. Stickstoff und Phosphor) und Baumwachstum an alpinen Baumgrenzen bisher deutlich unterschätzt. Im Untersuchungsgebiet weisen Analysen der C:N:P-Stöchiometrie in Böden und Blättern sowie von pflanzenverfügbarem N und P in Böden auf eine generelle Limitierung von N und P hin. Der Nährstoffmangel an N und P nimmt signifikant mit der Höhe [m ü. NN] zu und interagiert stark mit der Bestandsstruktur. Dies gilt auch für andere Nährstoffe (z.B. Kalium, Magnesium), sowohl in Böden als auch in Blättern. Nährstoffmangel kann demnach erklärend dafür sein, warum eine mögliche Verschiebung der Baumgrenze hangaufwärts und die globale Erwärmung entkoppelt sind (höhere

Bodentemperaturen an der Baumgrenze im Rolwaling im Vergleich zum globalen Durchschnitt).

Zusammenfassend hinterfragt die vorliegende Arbeit bisherige Studien, die argumentieren, dass alpine Baumgrenzen weder von der Verfügbarkeit an Bodennährstoffen noch von der Verfügbarkeit an Bodenfeuchte beeinflusst werden. Im Untersuchungsgebiet können sowohl bestimmte Kombinationen aus Bodeneigenschaften als auch einzelne Bodeneigenschaften allein Baumwachstum auch unterhalb der klimatischen Baumgrenze limitieren.

3 List of Publications

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

Manuscript 1, published as first author in *Progress in Physical Geography* 2016, Volume 40, Issue 1, Pages 135-160. doi: 10.1177/0309133315615802. Co-authors: Udo Schickhoff, Simon Drollinger, Jürgen Böhner, Ram Prasad Chaudhary, Thomas Scholten.
The full publication can be found on pages 68-110.

(2) Soil temperature and soil moisture patterns in a Himalayan alpine treeline ecotone *(accepted)*

Manuscript 2, accepted as first author in *Arctic, Antarctic, and Alpine Research* 2016, Volume 48, no. 3. Co-authors: Niels Schwab, Udo Schickhoff, Jürgen Böhner, Thomas Scholten.
The full publication can be found on pages 111-143.

(3) Soil and foliar C:N:P stoichiometry in an alpine treeline ecotone *(under review)*

Manuscript 3, under review as first author in *Geoderma* 2016. Co-authors: Yvonne Oelmann, Udo Schickhoff, Jürgen Böhner, Thomas Scholten.
The full publication can be found on pages 144-187.

(4) Nutrient deficiency in soils and trees of a treeline ecotone in Rolwaling Himal, Nepal *(under review)*

Manuscript 4, under review as Co-author in *Plant Ecology and Diversity* 2016. First author: Simon Drollinger. Co-authors: Timo Kobl, Niels Schwab, Udo Schickhoff, Thomas Scholten.
The full publication can be found on pages 188-214.

(5) Do Himalayan treelines respond to recent climate change? An evaluation of sensitivity indicators *(published)*

Manuscript 5, published as Co-author in *Earth System Dynamics* 2015, Volume 6, Pages 245-265. doi: 10.5194/esd-6-245-2015. First author: Udo Schickhoff. Co-authors: Maria Bobrowski, Jürgen Böhner, Birgit Bürzle, Ram Prasad Chaudhary, Lars Gerlitz, Helge Heyken, Jelena Lange, Thomas Scholten, Niels Schwab, Ronja Wedegärtner.
The full publication can be found on pages 215-264.

(6) Treeline responsiveness to climate warming: Insights from a krummholz treeline in Rolwaling Himal, Nepal *(published)*

Book chapter, published as Co-author in Singh ED, Schickhoff U, Mal S (eds) (2016): *Climate Change, Glacier Response, and Vegetation Dynamics in the Himalaya: Contributions toward Future Earth Initiatives.* Springer. Pages 307-346. First author: Niels Schwab. Co-authors: Udo Schickhoff, Lars Gerlitz, Birgit Bürzle, Jürgen Böhner, Ram Prasad Chaudhary, Thomas Scholten.
The full publication can be found on pages 265-315.

4 Introduction

Alpine treeline ecotones are characterised by extreme climate conditions and very limited resources (Wieser and Tausz, 2007; Holtmeier, 2009; Körner, 2012). 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. The 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.

Within the altitudinal zonation of vegetation in high mountains, the upper treeline (for detailed treeline terminology see Körner, 1998a, 2003a, 2012; Holtmeier, 2009) 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. When investigating alpine treelines, it is essential to distinguish between different spatial scales (Wilbanks and Kates, 1999; Malanson, 2011). 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. Körner, 1998a, b, 2007, 2012; Körner and Paulsen, 2004; Wieser and Tausz, 2007; Holtmeier, 2009). 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, soil moisture availability, geology and geomorphology, species dispersal and recruitment, plant morphology) which influence tree growth at its upper limit (e.g. Smith et al., 2003; Holtmeier and Broll, 2007, 2010; Macias-Fauria and Johnson, 2013; Sullivan et al., 2015). Therefore, 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 analysing the mechanisms locally. 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 analysing 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. Analysing relationships between soil properties and treeline spatial patterns is impeded by the fact that many treelines are strongly affected by human impact today (Miehe and Miehe, 2000; Holtmeier, 2009; 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).

Although a bulk of literature on treelines exists, only few specific soil-related studies have been conducted (e.g. Seastedt and Adams, 2001; Gruber et al., 2009a, b; Schmid et al., 2009; Liu and Luo, 2011; Dawes et al., 2014, 2015). Many studies focus on soil temperature (e.g. Aulitzky, 1960, 1961; Havranek, 1972; Körner, 1998a; Körner and Paulsen, 2004), whereas -related to the total amount of studies- only few authors also investigate treeline soil and foliar nutrient status (e.g. Köhler et al., 2006; Loomis et al., 2006; Li et al., 2008; Liptzin and Seastedt, 2009; Liptzin et al., 2012; McNown and Sullivan, 2013). Potential soil types and pedogenic processes occurring in treeline ecotones are discussed in greater detail for example in Stöhr (2007) and Holtmeier (2009), and in Bäumler (2015) with regard to the Himalaya. 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 (texture, bulk density) rarely appear in literature. In general, research on the effects of soil properties on tree growth at its upper limit is rather descriptive than quantitative.

4.1 Soil temperature at alpine treelines

Throughout diverse ecozones, soil temperature can be regarded as one of the fundamental soil properties that control tree growth. Several authors (e.g. 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 that low soil temperatures between 4 and 7°C affect tree growth by a reduction or an impediment of photosynthesis (e.g. Havranek, 1972; DeLucia, 1986; Day et al., 1989; Stöhr, 2007; Dong et al., 2011), root respiration and root water uptake (Walter and Medina, 1969; Walter, 1973; Benecke and Havranek, 1980; Mayr, 2007), root growth (e.g. Tranquillini, 1979; Alvarez-Uria and Körner, 2007; Stöhr, 2007; Treml et al., 2015), 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 (e.g. Tranquillini, 1979; Karlsson and Nordell, 1996; Karlsson and Weih, 2001; Kullman, 2007; Holtmeier, 2009).

A well accepted temperature threshold for tree growth at alpine treelines is the mean soil temperature during growing season (Körner and Paulsen, 2004; Körner, 2012). At a global scale, a growing season mean soil temperature of 6.4 ± 0.7°C at 10 cm soil depth 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.

Lower growing season mean soil temperatures under the closed forest compared to soil temperatures above the 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. Kessler and Hohnwald, 1998; Bendix and Rafiqpoor 2001; Bader et al., 2007; Oberhuber, 2007; Wieser and Tausz, 2007; Gruber et al., 2009b; Holtmeier and Broll, 2010). It has been shown that small-stature plants above treelines are decoupled from the 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; Körner 1998a, 2012; Doležal and Šrutek, 2002; Germino et al., 2002; Holtmeier, 2009).

According to Holtmeier (2009), this results in enhanced survival rates and reproduction when sufficient water and nutrients are provided.

However, despite an overall well documentation of soil temperatures at alpine treelines, data from the Himalaya are still marginally available. In particular, comprehensive soil temperature measurements including also subalpine forests and the alpine tundra do not exist.

4.2 Soil moisture at alpine treelines

Despite a low number of publications, soil moisture has frequently been named as an important soil property that affects tree growth in alpine treeline ecotones. With regard to ecozones, 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 that soil moisture does not affect tree growth at a global scale, which is in line with findings at a local scale (e.g. Neuwinger-Raschendorfer, 1963; Slatyer, 1976; Shrestha et al., 2007). At a local scale, however, soil moisture conditions and water availability can be highly variable due to small-scale mosaics of (micro-) topography (Ferrar et al., 1988), (micro-) climate, vegetation cover, and due to micro-scale variation in soil depth, type and structure (Broll et al., 2007; Wieser et al., 2009). Humus-rich upper horizons of forest soils, for example, had higher water-holding capacities and showed higher soil moisture than stony, coarse-grained soils above the treeline in Colorado, USA (Wardle, 1968). Further, the variation in snow pack and the onset of snowmelt determine 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. Peterson, 1998; Daniels and Veblen, 2004; Wilmking et al., 2006; Holtmeier and Broll, 2007; Shrestha et al., 2007; Batllori and Gutiérrez, 2008; Holtmeier, 2009; Richardson and Friedland, 2009; Barbeito et al., 2012).

Low soil water availability during different time periods of the year was found to affect tree growth and seedling establishment in all ecozones (Ferrar et al., 1988; Öberg and Kullman, 2012; Gaire et al., 2014; Liang et al., 2014; Piper et al., 2016), and particularly in arid and semi-arid subtropical or oceanic island treeline ecotones (Leuschner and Schulte, 1991; Gieger and Leuschner, 2004; Morales et al., 2004; Lara et al., 2005; Köhler et al., 2006; Fajardo et al., 2011). In contrast, high soil water contents were found to negatively affect tree growth at tropical treelines in Ecuador and Peru (Peters et al., 2014).

Therefore, the role of soil moisture for tree growth in alpine treeline ecotones is still uncertain. Soil moisture patterns vary considerably between different treeline ecotones, and between different ecozones. From the Himalaya, only a few studies exist, and, likewise to soil temperatures, a spatiotemporal soil moisture monitoring with focus also on the subalpine forests and the alpine tundra is not available.

4.3 Soil and foliar nutrients at alpine treelines

Since the biogeochemical cycles of carbon (C), nitrogen (N), and phosphorus (P) are coupled through the biochemical reactions during primary production, respiration, and decomposition (Finzi et al., 2011), soil and foliar C:N:P stoichiometry in alpine treeline ecotones can improve the understanding of nutrient availability and their potential limitation.

To date, soil nutrient availability and soil C:N:P ratios in alpine treeline ecotones are insufficiently explored. According to that, only a few concentrate on the nutrient status and availability in soils (e.g. Loomis et al., 2006; Zhang et al., 2011; Liptzin et al., 2012; McNown and Sullivan, 2013; Thébault et al., 2014; Sullivan et al., 2015). The majority of studies focus on nutrient uptake and investment by plants within alpine treeline ecotones (e.g. Körner, 1989; Karlsson and Nordell, 1996; Sveinbjörnsson, 2000; Birmann and Körner, 2009; Macek et al., 2012; Fajardo et al., 2012, 2013; Piper et al., 2016). Quantitative and experimental studies focusing on soil nutrients are rare, and tree physiological experiments for treeline species are missing.

Nitrogen (N) is considered as the most limiting nutrient to primary production in terrestrial plants (Vitousek and Howarth, 1991), including treeline trees (Haselwandter, 2007). However, several studies in different ecozones found even higher concentrations of N and C, such as sugars, starch, and lipids, in treeline trees compared to lower elevations (e.g. Weih and Karlsson, 2001; Shi et al., 2008; Fajardo et al., 2012, 2013). 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; Smith et al., 2003; Seastedt et al., 2004). The sink (growth) limitation hypothesis (Körner, 1998a, 2012) implies that suppression of meristematic activity can limit tree growth directly at low temperatures when photosynthesis is not necessarily limited. In accordance with this, higher foliar nutrient concentrations were said to support high metabolic activity (e.g. Weih and Karlsson, 2001; Shi et al., 2008; Fajardo et al., 2012, 2013). In contrast, the source (net photosynthesis) limitation hypothesis suggests that trees are unable to gain as much C or nutrients as they would be able to use for growth due to low nutrient availability or drought stress (Körner, 1998a, 2012; Sveinbjörnsson et al., 2010). In line with this, some studies from cool temperate, warm temperate, boreoarctic, tropical, subtropical, and oceanic treelines detected lower foliar N concentrations due to lower soil N availability at treeline compared to lower elevations (e.g. Köhler et al., 2006; Huber et al., 2007; McNown and Sullivan, 2013; Sullivan et al., 2015). In general, an increase in photosynthesis, and thus C assimilation can only be guaranteed by an appropriate availability of soil N, which is essential in generating high-energy compounds such as ATP and NADPH during photosynthesis. Negative elevational gradients in nutrients were interpreted to mainly result from cold soil temperatures and poor soil quality which lead to slower rates of potential soil respiration, reduced photosynthesis, hampered litter decomposition including soil N mineralization, and constrained growth of treeline trees (Sveinbjörnsson, 2000; Loomis et al., 2006; Huber et al., 2007; McNown and Sullivan, 2013). In turn, tree vegetation itself influences pedogenesis and thus soil nutrient conditions by amount, coverage and quality of litter (Shiels and Sanford, 2001; Holtmeier and Broll, 2007; Stöhr, 2007; Holtmeier, 2009). Furthermore, trees or tree stands control soil temperatures and soil moisture, and thus root growth, nutrient uptake, and decomposition including mineralisation (Broll and Holtmeier, 1994; Holtmeier and Broll, 2007; Stöhr, 2007; Holtmeier, 2009). For example, alpine tundra soils were characterised as areas with low mineralisation rates of SOM due to prevalent cold and dry conditions, which constrain nutrient supply, and in turn limit plant production (e.g. Bowman et al., 1993; Liptzin and Seastedt, 2009). Finally, microorganisms outcompeted trees in terms of uptake of limiting soil nutrients (N) serving as a potential cause for limited tree growth in alpine treeline ecotones (Liu et al., 2012; Thébault et al., 2014).

Previous studies not originating from alpine treelines found a changing soil C, N, and P supply, and thus changing foliar stoichiometric ratios with altering climatic conditions such as temperature or precipitation (e.g. Walker and Syers, 1976; McGill and Cole, 1981; Reich and Oleksyn, 2004). This suggests potential shifts in the stoichiometric coupling of soil and foliar C, N, and P concentrations in alpine treeline ecotones, where climatic conditions (e.g. decreasing temperatures) are different compared to lower elevations. Alterations in the foliar C:N:P stoichiometry have been shown to be species-specific as it is inherently occurring at a global scale, i.e. some tree species show nutrient concentrations proportional to the nutrient source (stoichiometric plasticity), whereas others are characterised by consistently regulated nutrient concentrations independent of changing soil nutrient availability (stoichiometric homoeostasis) (Sterner and Elser, 2002; Zhang et al., 2013; Sardans et al., 2015). These relationships were expressed in the T-Biogeochemistry hypothesis (Reich and Oleksyn, 2004), which stated that the soil nutrient availability depending on temperatures has effects on the foliar nutrient concentrations. Thus, individual species may react in different ways to potential altitudinal changes in soil nutrient availability and soil stoichiometry at a local scale. With regard to alpine treeline ecotones, these processes are not well explored, pointing to research deficits.

5 Objectives

This thesis seeks to investigate the interactions among soil properties and variations in stand structures and tree physiognomy in the Rolwaling alpine treeline ecotone. Since soil properties are generally heterogeneous and highly variable amongst different alpine treeline ecotones worldwide, and even at microscale within the individual ecotones, a spatiotemporal soil analyses of high resolution was performed. Thus, in a first step, this thesis focuses on the general effects of soil properties on tree growth in alpine treeline ecotones (Manuscript 1). The main part of this thesis investigates the local scale interactions among soil temperature, soil moisture (Manuscripts 1, 2, 5; Book chapter) and soil nutrients (Manuscripts 1, 3, 4), respectively, and variations in stand structures and tree physiognomy.

In detail, this thesis has the following objectives:

(i) to review how soil properties affect tree growth at its upper limit, both in global and local perspectives, and to identify soil variables -also with regard to regions- that have not gained adequate attention yet (Manuscript 1);

(ii) to examine the interactions among soil temperature and soil moisture, and variations in stand structures and tree physiognomy in the Rolwaling treeline ecotone (Manuscripts 1, 2, 5; Book chapter);

(iii) to test the interactions between altitudinal changes in stand structures and tree physiognomy, and (a) the soil nutrient availability, (b) the foliar nutrient concentrations, (c) the soil and foliar C:N:P stoichiometry, and (d) the relationships between soil stoichiometry and soil nutrient availability, and foliar stoichiometry (Manuscripts 1, 3, 4).

According to the objectives, a specific experimental design was necessary. The ”TREELINE” research project provided the framework for this thesis. The “TREELINE” project is an interdisciplinary research group investigating the effects of climate warming on the sensitivity and response of the Rolwaling treeline ecotone. In this context, this thesis contributes important findings with regard to soil-alpine treeline ecotone interactions.

6 Methods

6.1 Study area and experimental design

The Rolwaling valley in the northeast part of Central Nepal (N 27°54’, E 86°22’; Fig. 1a) is characterised by a warm temperate climate with cool summers and dry winters. From June to September, it is intensively affected by the South-Asian summer monsoon. In 2014, four different climate stations (Fig. 1a) measured mean annual temperatures from 2.8 to 3.6°C, and annual precipitation sums from 1042 to 1316 mm. Bedrock is granite and gneiss containing a low proportion of P (< 0.2 mass% P_2O_5). Topography is characterised by generally steep slopes with a mean inclination of 37°. Creeks and gullies frequently cut deep into these slopes. Soils were classified as Podzols (IUSS, 2006), characterised by a substantial outwash primarily of soil organic matter (SOM) and sesquioxides (Al, Fe) from topsoils to subsoils (podsolization). Soils have generally low pH, slightly increasing with soil depth (from 2.5 to 4). Podzols show the typical sequence of Oi-Oe-Ah-Ae-Bh-Bs. Soil depths vary from 30 to 70 cm, with an overall high proportion of skeletal fractions (e.g. 75 to 95% in Ae).

Subalpine forests are primarily composed of *Abies spectabilis* and *Betula utilis*, with *Acer caudatum*, *Rhododendron campanulatum* (*Rhc*), and *Sorbus microphylla* forming a second tree layer (see Manuscript 5 and Book chapter). Upslope, the forests convert into an extensive krummholz belt of *Rhc* (3900 m a.s.l. in NW exposition; 4000 m a.s.l. in NE exposition; cf. Fig. 2), which turns into alpine dwarf scrub heaths of *Rhododendron anthopogon* and *Rhododendron setosum* (*Rhas*) at 4000 m a.s.l. and 4100 m a.s.l., respectively. Dwarf shrubs are interspersed by low growing individuals (diameter at breast height, dbh < 7 cm) or young growth of *Abies*, *Betula*, and *Rhc*. Here, scattered *Sorbus* individuals with dbh ≥ 7 cm occur. Ground cover vegetation and species richness decrease from the closed subalpine forests across the treeline ecotone. The occurring tree and shrub species are prevailing shallow rooting plants (ca. 0-20 cm, own observations). Due to the isolation and a very low population density of the Rolwaling valley, and virtually pristine vegetation, the treeline ecotone is considered as near-natural.

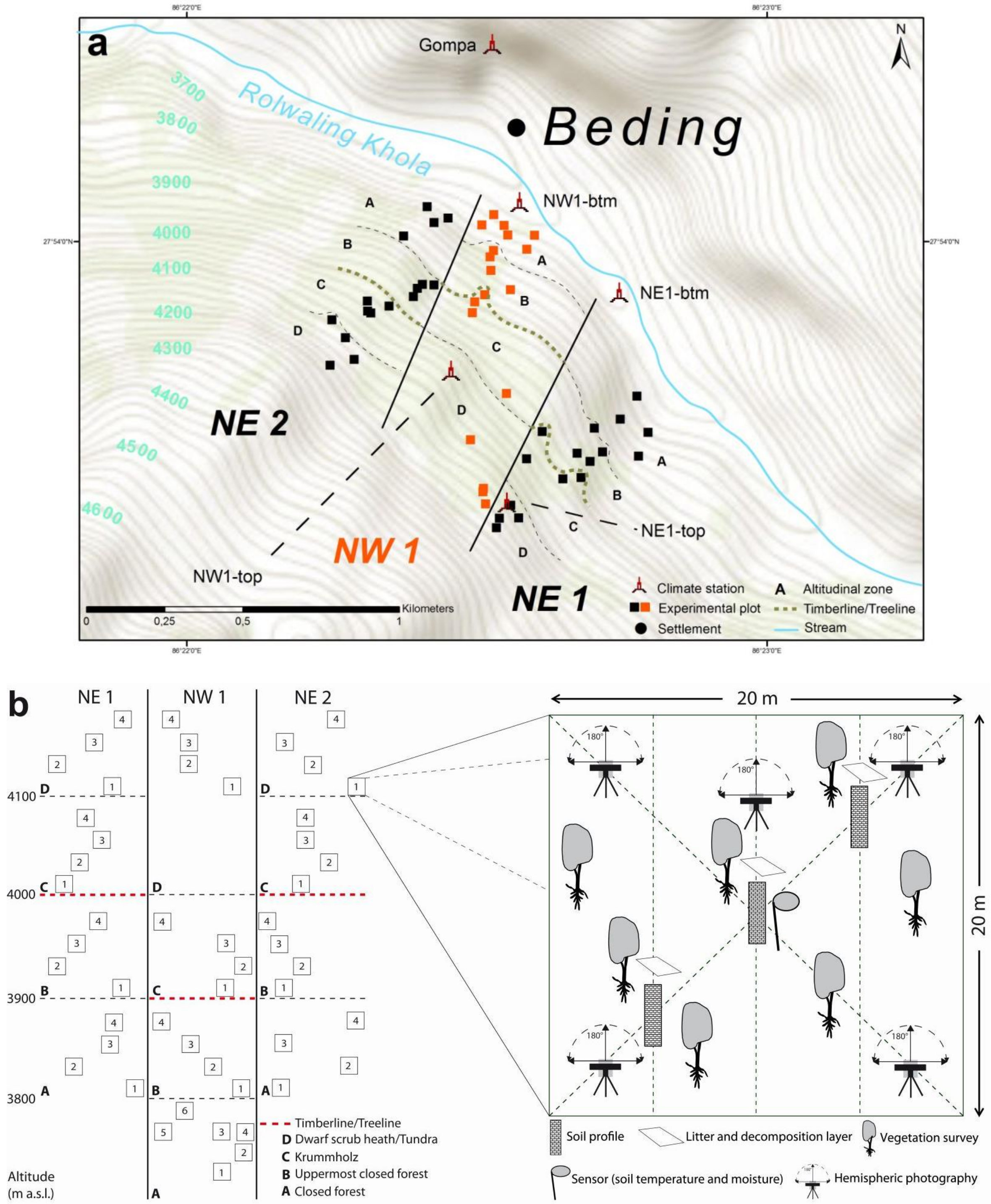

Figure 1. Study area and experimental design (a) including topography, location of altitudinal zones (A, B, C, D) and experimental plots as part of three altitudinal transects (NE1 = Northeast 1, NW1 = Northwest 1, NE2 = Northeast 2), and location of climate stations (btm = bottom, top). (b) Schematic illustration of the three altitudinal transects including four experimental plots (20 m x 20 m) in each altitudinal zone (left). Plot design is equivalent on each plot (right). Soil temperature and moisture sensors were installed on NW1 and NE2 only. The altitudinal transects in (a) and (b) (left) are mirror-inverted.

The experimental area is situated on the unsettled north-exposed slope opposite to the village of Beding (Figs. 1a, 2). A stratified random experimental design was used with three transects (NE1 = Northeast 1, NW1 = Northwest 1, NE2 = Northeast 2; Figs. 1a, b) across the treeline ecotone divided into four altitudinal zones: A (subalpine forest), B (uppermost subalpine forest), C (krummholz), and D (dwarf scrub heath or alpine tundra; Figs. 1a, b). Within each zone of each altitudinal transect, four different experimental plots (20 m x 20 m; projected on a horizontal plain) were randomly selected (Figs. 1a, b). Transect NW1 has two additional plots in zone A. In total, 50 experimental plots were specified. On the two NE transects, altitudinal zone A ranges from 3800 to 3900 m a.s.l., followed by B (3900 to 4000 m a.s.l.), C (4000 m to 4100 m a.s.l.), and D (4100 m to 4240 m a.s.l.). According to the occurring vegetation, the zones are located 100 m lower in elevation on NW1 (Figs. 1a, b, 2).

Figure 2. Study area with the alpine treeline (3900 – 4000 m a.s.l.) on the north-facing slope on the opposite side of the village Beding (lower left). (Photo: Schwab, 18 September 2014; Photo taken from Manuscript 5).

6.2 Data collection

Three soil profiles were examined on each of the 50 experimental plots (Figs. 1a, b), according to the German soil classification (Ad-hoc-Arbeitsgruppe Boden, 2005). From these soil profiles, the respective mineral soil horizons (Ah, Ae, Bh, Bs) were combined to composite samples during four different field campaigns (May 2013 and 2014, September 2014 and 2015) resulting in a total of 632 samples. Additionally, three organic layer samples of each the Oi and Oe layers were collected in May 2013 and 2014. Moreover, foliage of the living evergreen tree species *Abies* and *Rhc* as well as the evergreen shrub species *Rhas* were sampled above the soil profiles. Sampling took place at the onset of May 2013 and 2014, and in September 2014 and 2015. Additionally, the deciduous tree species *Acer*, *Betula*, and *Sorbus* were sampled in September 2014 and 2015.

Vegetation surveys took place in April, May, July and August 2013, and in September 2014, when dbh (at 130 cm above ground), and tree height of all trees with dbh ≥ 7 cm were measured (see Book chapter). Crown length (length of crown from trunk to terminal bud), and crown width were determined according to van Laar and Akça (2007). The number of tree individuals (dbh ≥ 7 cm) was counted on each experimental plot. Leaf area index (LAI) was measured using hemispheric photography, and HemiView software (HEMIv9, Delta-T devices, UK). The camera (Nikon Coolpix 8400) included a wide-angle fisheye lens (Nikon Fisheye Converter FC-E9), which was aligned to the free sky obtaining an angle of view of 180°. Five photos per experimental plot (Fig. 1b) were taken in a cross pattern at 90 cm above ground at consistent clouded sky to enable an optimal documentation of light conditions. Photos were taken from 22.09.2014 to 27.09.2014 on NW1, and from 09.09.2014 to 21.09.2014 on NE2. The vegetation parameters used in this thesis are presented in Table 1 as means in each altitudinal zone (NW1 and NE2 transect).

On 32 plots along NW1 and NE2, *WiFi Plant Sensors* (Koubachi Inc., Switzerland) recorded soil temperature (°C) and soil moisture (pF) every hour at 10 cm depth from May 2013 to October 2015. Additionally, two sensors were placed underneath the uppermost individuals of *Abies* and *Betula* on NE2 (equivalent to the transition from zone B to C). The aim was to obtain data from two different expositions. Thus, no sensors were installed on NE1. The sensors were modified for outdoor usage to log soil temperature from –10°C to +55°C, and pF (decadic logarithm of the absolute value of soil water tension, non-dimensional) from 0 to 5.75. Lithium batteries were used, which ensured energy supply under harsh climatic conditions. Data were obtained via *WiFi* interface. For the calculation of growing season mean soil temperatures, the well-accepted definition of growing season by Körner and Paulsen (2004) was used, when daily mean soil temperatures at 10 cm depth first exceeded 3.2°C until they dropped again below 3.2°C. Soil moisture was determined as soil water content (SM; 0-10 cm; Vol.-% or L m^{-2} dm^{-1}) from pF based on linear regression equations derived from default charts of the German soil classification (Ad-hoc-Arbeitsgruppe Boden, 2005), and as available water capacity (AWC, 0-10 cm; Vol.-% or L m^{-2} dm^{-1}) from soil water content, soil texture and bulk density according to the German soil classification (Ad-hoc-Arbeitsgruppe Boden, 2005).

Since spring 2013, seven climate stations (HOBO U30-NRC; ONSET Computer Corporation, USA) measure air temperature (°C), precipitation (mm), humidity (%), wind (m s^{-1}), and solar radiation (W m^{-2}) in a 15 minutes interval.

6.3 Laboratory analyses

Soil samples were analysed for total C (equal to C_{org}, according to the geology), total N, plant-available N (N_{min}), total P, plant-available P (P_{av}), pH, and effective cation exchange capacity (natrium, Na; potassium, K; magnesium, Mg; calcium, Ca; manganese, Mn; iron, Fe; aluminium, Al). From litter and foliage, the nutrient concentrations of C, N, P, Na, K, Mg, Ca, Mn, Fe, and Al were measured. Total C and N of soils, foliage, and organic layers (Oi, Oe) were determined using elemental analyzer (vario EL II; Elementar, Germany). For analysis of soil N_{min} (NO_3^-, NH_4^+), an aliquot of 10 g of homogenised field-fresh soil with 1 M KCl solution was shaken rigorously every 15 minutes for one hour. The extraction solution was filtered, and acidified with HCl, subsequently. N_{min} fractions were analysed in the laboratory by continuous flow analysis (CFA, SEAL Auto Analyzer AA3 HR; SEAL Analytical Inc., UK). Total P and plant-available P of soil samples were assessed following a modified protocol of Hedley et al. (1982). The sequential extraction of P was reduced to four steps where the extracted fractions comprised 0.5 M $NaHCO_3$-P_i and -P_o (labile), 0.1 M NaOH- P_i and -P_o (moderately labile), 1 M concentrated HCl-P, and 0.5 M H_2SO_4-P (both stable). In each extraction solution, inorganic P fractions (P_i) were measured with CFA, and organic P fractions (P_o) with ICP-OES (Perkin Elmer Optima 5300 DV; Perkin Elmer, USA). A study by Hacker et al. (submitted) showed the strongest relationship with microbial P (as soil component relevant for stoichiometric considerations) for the sum of labile and moderately labile P_i and P_o concentrations (expressed as P_{av} in this thesis). pH of soils was 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; WTW Inc., Germany). Na, K, Mg, Ca, Mn, Fe, Al, and P concentrations (expressed per unit of dry biomass, mg g^{-1}) in litter and foliage were measured with ICP-OES after microwave-digestion (MLS START 1500 Microwave Extractor; EVISA, Germany; extracts: 4 ml HNO_3, 3 ml H_2O_2, 5 ml H_2O). Soil texture (Table 1) was analysed according to Blume et al. (2011), using a Sedigraph III Plus Particle Size Analyzer (Micromeritics Inc., Germany). Bulk density (Table 1) was determined gravimetrically after field sampling with 100 cm^3 core cutters and soil drying at 105°C.

Table 1. Summary of vegetation, soil texture, and bulk density data (means of altitudinal zones ± s.e.). dbh = diameter at breast height. NE2 = Northeast 2 transect, NW1 = Northwest 1 transect. A, B, C, D = Altitudinal zones. Different letters indicate significant differences at $P < 0.05$ by Post hoc Nemenyi (Tukey) test.

Transect - Altitudinal zone	**Tree height**	**Crown width**	**Crown length**	**dbh**	**Individuals (dbh ≥ 7 cm)**	**Leaf area index**	**Sand**	**Silt**	**Clay**	**Bulk density**
	[m]	[m]	[m]	[cm]	[n]	[LAI]	[%]	[%]	[%]	[g cm^{-3}]
NE2 – A	7.84 ± 1.13^{a}	4.24 ± 0.33^{a}	4.08 ± 0.74^{a}	16.59 ± 2.13^{a}	50 ± 18^{a}	1.74 ± 0.17^{a}	65 ± 2^{a}	27 ± 1^{a}	8 ± 2^{a}	1.24 ± 0.17^{a}
NE2 – B	5.66 ± 0.52^{a}	3.61 ± 0.36^{a}	3.08 ± 0.28^{a}	14.02 ± 0.72^{a}	96 ± 23^{b}	1.88 ± 0.22^{a}	63 ± 4^{a}	28 ± 2^{a}	9 ± 1^{a}	1.14 ± 0.09^{ab}
NE2 – C	1.94 ± 0.86^{b}	2.35 ± 0.13^{b}	0.82 ± 0.22^{b}	7.90 ± 0.44^{b}	40 ± 36^{a}	1.47 ± 0.14^{a}	68 ± 5^{a}	24 ± 4^{a}	8 ± 1^{a}	1.10 ± 0.11^{a}
NE2 – D	0.55 ± 1.10^{c}	0.38 ± 0.75^{c}	0.31 ± 0.63^{c}	1.83 ± 3.65^{c}	1 ± 1^{c}	0.14 ± 0.07^{b}	73 ± 6^{a}	19 ± 5^{a}	8 ± 3^{a}	0.97 ± 0.01^{b}
NW1 - A	5.64 ± 0.34^{a}	3.58 ± 0.53^{a}	3.24 ± 0.20^{a}	11.62 ± 1.86^{a}	42 ± 19^{a}	1.49 ± 0.16^{a}	65 ± 1^{a}	27 ± 1^{a}	8 ± 1^{a}	1.20 ± 0.17^{a}
NW1 - B	5.46 ± 0.74^{a}	4.03 ± 1.06^{a}	3.35 ± 0.85^{a}	13.90 ± 2.04^{a}	45 ± 13^{a}	1.35 ± 0.13^{a}	61 ± 1^{a}	30 ± 2^{a}	9 ± 1^{a}	1.38 ± 0.08^{a}
NW1 - C	2.47 ± 0.38^{b}	2.26 ± 0.15^{b}	1.10 ± 0.36^{b}	8.63 ± 0.68^{b}	105 ± 60^{b}	1.27 ± 0.27^{a}	69 ± 7^{a}	24 ± 6^{a}	7 ± 2^{a}	1.20 ± 0.14^{a}
NW1 - D	0.53 ± 1.05^{c}	0.28 ± 0.56^{c}	0.25 ± 0.50^{c}	1.78 ± 3.55^{c}	1 ± 2^{c}	0.11 ± 0.02^{b}	69 ± 7^{a}	23 ± 5^{a}	8 ± 2^{a}	1.07 ± 0.11^{a}

6.4 Data processing

Statistical analyses were conducted using the free programming language R, version 3.1.2 (R Development Core Team, 2014) by applying the R-packages *car* (Fox and Weisberg, 2011), *MASS* (Venables and Ripley, 2002), *methods* (R Development Core Team, 2014), *nortest* (Gross and Ligges, 2012), *PMCMR* (Pohlert, 2014), *relaimpo* (Grömping, 2006), *shape* (Soetaert, 2014), *stats* (R Development Core Team, 2014), *vegan* (Oksanen, 2015), and *zoo* (Zeileis and Grothendieck, 2005).

To ensure **objective (i)** of this thesis, in a first step the literature databases Web of Science (WoS), and Bielefeld Academic Search Engine (BASE) were used to search for alpine treeline-related literature (for search terms see Manuscript 1). In a second step, a literature review of 507 studies determined the importance of various treeline-controlling factors as well as underlying processes, and subordinate factors at different spatial scales. A 5-category rating of treeline-controlling factors was carried out, which was based on the findings of the respective author(s). In case the explanatory power of potential factors was evaluated by the author(s), their ranking of factors was followed, and was converted into five categories. In all other cases, their findings were assigned into five categories graduating the factors from a very high to very low effect on tree growth at its upper limit. The number of tallies was weighted 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 characterise 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 standardised to 100 % (equation c). The same calculations were applied to single ecozones to analyse the relative importance of factors for tree growth in the respective ecozone.

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

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

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

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

Considering **objective (ii)** of this thesis, the generally small data gaps (< 15 days) of soil temperature and soil pF were interpolated and extrapolated using the R-packages *zoo* and *stats* in a first step. Data were transferred to ArcMap 10.1, and georeferenced based on GPS data generated during fieldwork. In ArcMap, IDW (Inverse Distance Weighting) was used as deterministic method for spatial interpolation (Figs 5, 6). In a second step, multivariate statistical analyses were performed to test the relations between the independent soil variables temperature (ST) and available water capacity (AWC), and the dependent vegetation variables tree height, dbh, crown width, crown length, number of tree individuals, and LAI. Due to multicollinearity, soil water content (SM) was excluded from the analyses. The large datasets of ST and AWC contained the means from each experimental plot on the NE2 and NW1 transects (NE2-A1 to NE2-D4, NW1-A1 to NW1-D4), respectively, for the entire measurement period (01.05.2013 – 31.10.2015), and for the different seasons (MAM 14, 15, JJAS 13, 14, 15, ON 13, 14, DJF 13/14, 14/15, see 7.2 and 7.3). For the dependent variables, plot means were used. Statistical analyses initially consisted of Principal Component Analyses (PCA) for each of the two datasets ST and AWC individually. The reasons for that were to avoid multicollinearity among the many variables that represented the datasets, and to create the best fitting model of principal components for each of the two variables before a Redundancy Analysis (RDA) was performed. Using the principal components in a RDA, the effects of ST and AWC on vegetation variables were tested with regard to the diverse altitudinal zones (A, B, C, D), and to different expositions (NW, NE) (Fig. 7). To verify the RDA results, a Multivariate Multiple Regression analysis (MMR) with subsequent MANOVA and ANOVA was additionally applied. In a third step, the inverse effects of environmental variables on ST, AWC, and SM were tested using MMR and Multiple Linear

Regression analyses (MLR). For that reason, a larger dataset was included consisting of the vegetation variables used above, complemented by various soil-related variables (texture, bulk density, Table 1; thickness of litter layer, see 7.5.3) and topographical variables (aspect: northness = cos (exposition); elevation [m a.s.l]). To avoid multicollinearity between the independent variables, they were tested using the *vif.cca* function in R. To create the best fitting model (MMR) explaining all dependent variables, and each dependent variable individually (MLR), a stepwise backward selection was conducted using the *ordistep* function from the *vegan* package in R.

In view of **objective (iii)** of this thesis, first potential significant ($P < 0.05$ hereafter) differences among the altitudinal zones A, B, C, and D were tested for both soil N (Table 5) and P (Tables 4, 5) availability, soil and foliar C, N, and P, and their ratios (Tables 5, 6), and soil and foliar Na, K, Mg, Ca, Mn, Fe, and Al concentrations using a one-way ANOVA or a Kruskal-Wallis test depending on the Gaussian distribution and homogeneity of variance of the data. The significance of differences was examined by applying a Post hoc Tukey HSD test or a Post hoc Nemenyi (Tukey) test. Second, potential changes in soil and foliar C, N, and P, and their ratios with elevation [m a.s.l.] were tested using the Spearman correlation analysis and linear regression analyses. Third, to determine the relationships between soil stoichiometry and soil nutrient availability, and foliar stoichiometry, MLR and bivariate linear regression analyses were performed. Significant effects of topsoil C, N, P_{av}, C:N, C:P, N:P, and N_{min} on foliar C, N, P, C:N, C:P, and N:P, respectively were tested (Table 7; Fig. 10). We chose topsoil variables, since it was the largest dataset, and the tree and shrub species mainly root in this part of the soils. The multiple analyses included stepwise backward regression, where the variables were excluded stepwise from the analyses that did not contributed significantly to the explained variation. This method was applied to the six species *Abies, Acer, Betula, Rhas, Rhc,* and *Sorbus* separately.

7 Results

7.1 Evaluation of soil properties affecting alpine treelines

According to the literature review of 507 treeline studies, soil temperature was found to be the factor with the second highest relative importance after air temperature for tree growth at its upper limit, both at a global and at a local scale (Fig. 3a). Soil moisture was among the most discussed factors, and was supposed to have the fourth highest relative importance for tree growth, however greater at a local (7.7 %) than at a global scale (4.2 %; Fig. 3a). Soil and foliar nutrients (primarily N and P) were underrepresented with a relative importance for tree growth of 5 % at a global and a local scale compared to soil temperature (10 %) and soil moisture (7 %; Fig. 3a). This concerned also soil physical properties (e.g. texture, organic matter quality) and C balance / limitation with relative importances for tree growth below 5 % (Fig. 3a). Other factors that influence acquiring and recycling of nutrients in soils like mineral weathering, frost-thaw-cycling (permafrost-affected soils), soil microorganisms, and mycorrhizal funghi were highly underrepresented in treeline literature (excluded from Figs. 3a, b).

Major differences in the relevance of treeline-controlling factors for tree growth were found in different ecozones (Fig. 3b). According to the existing literature, soil temperature plays a major role at tropical, subtropical, cool temperate and boreoarctic treelines, but has not been named as controlling factor at oceanic treelines (Fig. 3b). Soil moisture deficits and seasonal drought stress are assumed to be crucial in particular at oceanic, and semi-arid and arid subtropical treelines (Fig. 3b). The amount of studies dealing with soil and foliar nutrients, and especially with soil physical properties related to the total amount of publications was very small. The review also exposed that the number of studies in some ecozones (especially Subtropics, Mediterranean and oceanic islands) are few and thus make it difficult to understand the constraints on tree growth in such regions and to relate those to findings in other ecozones or in a global perspective (see Manuscript 1).

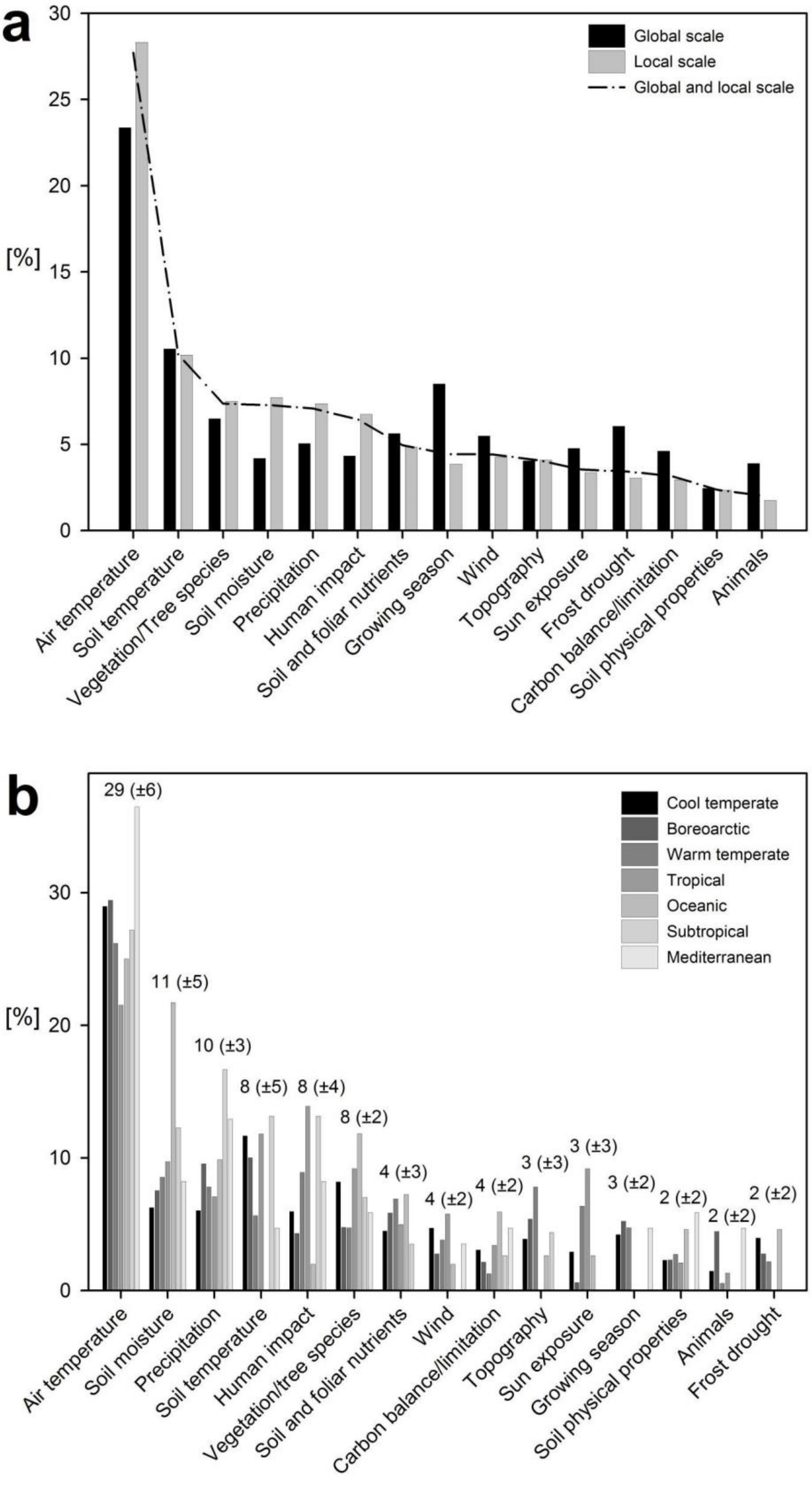

Figure 3. Relative importance [%] of factors controlling tree growth at its upper limit regarding (a) different spatial scales and (b) different ecozones. Studies including different spatial scales (miscellaneous) are excluded from Figure 3(b). Mean ± s.e. is given for each ecozone.

7.2 Soil temperature patterns in Rolwaling

In the study area, mean soil temperatures (period: 01.05.2013 – 31.10.2015) at 10 cm depth showed a significant decrease with elevation [m a.s.l.] on the NW1 transect (Spearman r = -0.71, p < 0.01). In contrast, no significant decrease was detected on the NE2 transect (r = -0.04, p = 0.88). Also during growing season (Fig. 4), NW1 showed a significant decline of mean soil temperatures with elevation [m a.s.l.] (2013: r = -0.74, p < 0.001; 2014: r = -0.82, p < 0.01; 2015: r = -0.81, p < 0.001) which was not found on NE2 (2013: r = 0.15, p = 0.55; 2014: r = -0.01, p = 0.99; 2015: r = 0.28, p = 0.25). Despite altitudinal zones A-D are located 100 m lower in elevation [m a.s.l. on NW1 (Figs. 1a, b), mean soil temperatures during growing season were slightly lower along the entire NW1 transect (A-D) (2013: 7.7 ± 0.8°C, 2014: 7.4 ± 0.8°C, 2015: 7.4 ± 0.7°C) compared to NE2 (2013: 7.8 ± 0.6°C, 2014: 7.7 ± 0.6°C, 2015: 7.5 ± 0.6°C). At treeline (transition from B to C) a growing season mean soil temperature of 7.5 ± 0.6°C was calculated as mean of both transects for the growing seasons in 2013, 2014, and 2015 –normal years with respect to meteorological events in the study area. Hereby, the mean soil temperatures at treeline were slightly higher or the same on NW1 compared to NE2 (Fig. 4).

Besides, altitudinal zone-specific spatial patterns of mean soil temperatures were found. On NW1, the mean soil temperatures (period: 01.05.2013 – 31.10.2015) showed a strong decline from AB (4.56°C, 4.76°C) to CD (3.29°C, 2.95°C). On NE2, a temperature gradient occurred from AB (4.05°C, 4.68°C) to C (3.28°C), however a higher mean temperature was measured in D (4.17°C). A variance analysis (Kruskal Wallis) with subsequent Post-hoc Nemenyi (Tukey) test revealed major differences (p < 0.0001) in daily mean soil temperatures between altitudinal zones on both transects. On NW1, zones A and B (p = 0.28), and C and D (p = 0.12) showed similar variances. On NE2, zones A and D (p = 0.66), and B and D (p = 0.30) did not differ significantly from each other.

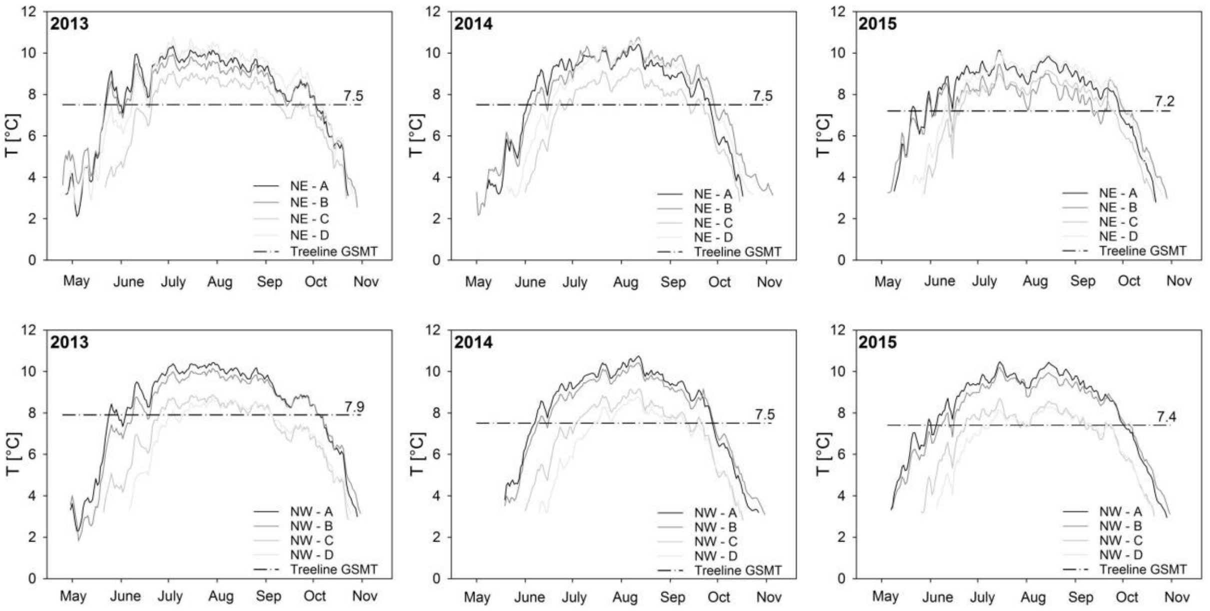

Figure 4. Daily mean soil temperatures during growing season in 2013, 2014, and 2015 at 10 cm depth in altitudinal zones A (closed forest), B (uppermost closed forest), C (krummholz), and D (alpine tundra) on NE2 (NE, top) and NW1 transect (NW, bottom). Treeline GSMT = Growing season mean temperature at 10 cm soil depth at treeline.

With regard to different seasons, the mean soil temperatures in spring (MAM) were commonly higher on NE2 (Table 2, Fig. 5). An opposite spatial trend was found in autumn (ON) and winter (DJF), except for the alpine tundra (D) (Table 2). In summer (JJAS), temperature was similar on both transects, except for the alpine tundra where NE2 was marked by on average 2 Kelvin higher temperatures than NW1 (Table 2, Fig. 5).

In summary, year-round higher soil temperatures were measured in D compared to C, and slightly higher or similar soil temperatures compared to A on NE2. This was not found for NW1, where the lowest soil temperatures occurred in D, especially in summer (JJAS). Higher soil temperatures in D compared to C were found in ON 13 and DJF 13/14 only, and similar soil temperatures were measured in MAM 14. On both transects, winter (DJF) soil temperatures were similar or even colder in A compared to C and D, and were warmest in B (Fig. 5). Also in autumn (ON) and spring (MAM), higher soil temperatures were measured in B compared to A. In general, soil temperatures in winter 2014/2015 (DJF 14/15) were markedly higher than in winter 2013/2014 (DJF 13/14). Likewise, the soil temperatures in spring 2015 (MAM 15) exceeded those in spring 2014 (MAM 14).

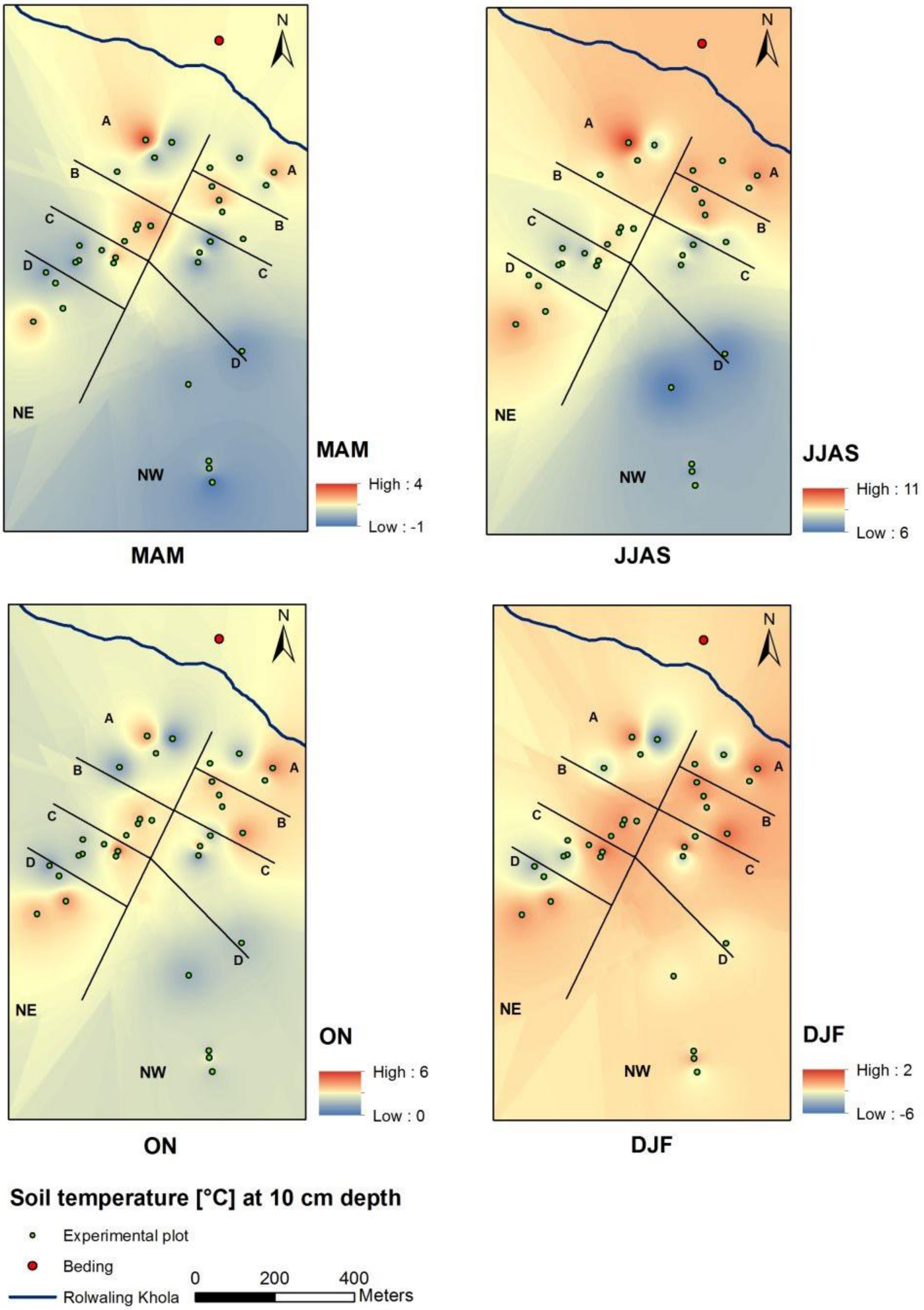

Figure 5. Spatiotemporal distribution of soil temperatures [°C] at 10 cm depth. A, B, C, D = Altitudinal zones. NW = Northwest, NW1. NE = Northeast, NE2. MAM = spring (March, April, May), JJAS = summer (June, July, August, September), ON = autumn (October, November), DJF = winter (December, January, February).

Table 2. Mean (± s.e.) soil temperatures [°C] at 10 cm depth in the altitudinal zones A, B, C, and D on the NE2 and NW1 transect. AM 13 = April-May 2013, MAM = spring (March, April, May). JJAS = summer (June, July, August, September), ON = autumn (October, November), DJF = winter (December, January, February). Different letters indicate significant differences at $P < 0.05$ by Post hoc Nemenyi (Tukey) test.

Transect	Season	A	B	C	D
NE2	AM 13 [1]	4.4 ± 1.2 ^{a}	5.1 ± 0.7 ^{b}	2.5 ± 1.2 ^{c}	4.7 ± 0.7 ^{d}
	JJAS 13	9.2 ± 1.2 ^{a}	8.9 ± 0.5 ^{b}	7.9 ± 0.7 ^{c}	9.4 ± 0.7 ^{a}
	ON 13	2.5 ± 1.6 ^{a}	3.3 ± 1.0 ^{ab}	2.3 ± 0.4 ^{bc}	2.9 ± 1.6 ^{c}
	DJF 13/14	-2.9 ± 2.0 ^{a}	-0.6 ± 0.7 ^{b}	-3.2 ± 1.5 ^{a}	-2.6 ± 2.0 ^{c}
	MAM 14	1.2 ± 1.5 ^{ab}	1.9 ± 0.8 ^{b}	0.2 ± 0.8 ^{a}	1.0 ± 1.0 ^{b}
	JJAS 14	9.1 ± 1.2 ^{a}	9.2 ± 1.2 ^{a}	7.6 ± 0.8 ^{b}	8.9 ± 0.6 ^{a}
	ON 14	2.0 ± 1.6 ^{a}	3.5 ± 0.8 ^{b}	1.9 ± 0.4 ^{b}	2.8 ± 1.5 ^{c}
	DJF 14/15	-1.7 ± 2.5 ^{a}	0.0 ± 0.4 ^{b}	-1.1 ± 1.2 ^{c}	-0.8 ± 1.9 ^{c}
	MAM 15	1.5 ± 1.9 ^{ac}	2.3 ± 0.8 ^{bd}	0.5 ± 0.7 ^{acd}	0.9 ± 1.1 ^{bcd}
	JJAS 15	8.8 ± 1.5 ^{a}	8.0 ± 0.6 ^{b}	7.8 ± 0.7 ^{b}	8.7 ± 0.4 ^{a}
NW1	AM 13 [1]	4.2 ± 1.0 ^{a}	3.7 ± 1.2 ^{b}	2.8 ± 1.1 ^{c}	1.3 ± 0.7 ^{d}
	JJAS 13	9.5 ± 0.6 ^{a}	9.2 ± 0.7 ^{b}	7.7 ± 1.0 ^{c}	7.3 ± 0.9 ^{c}
	ON 13	3.2 ± 1.1 ^{ab}	3.9 ± 0.3 ^{bc}	2.4 ± 1.2 ^{c}	2.7 ± 0.6 ^{c}
	DJF 13/14	-1.9± 1.8 ^{a}	-0.8 ± 0.9 ^{b}	-2.4 ± 1.8 ^{a}	-2.1 ± 1.1 ^{a}
	MAM 14	0.8 ± 1.0 ^{a}	1.3 ± 0.8 ^{b}	0.0 ± 1.1 ^{a}	0.0 ± 0.6 ^{a}
	JJAS 14	9.3 ± 0.6 ^{a}	9.0 ± 0.8 ^{a}	7.4 ± 1.1 ^{b}	6.7 ± 0.6 ^{c}
	ON 14	3.0 ± 1.3 ^{a}	3.7 ± 1.0 ^{b}	2.0 ± 1.2 ^{b}	1.6 ± 0.6 ^{b}
	DJF 14/15	-0.2 ± 1.5 ^{a}	0.6 ± 1.2 ^{b}	-0.6 ± 1.6 ^{a}	-1.1 ± 0.7 ^{c}
	MAM 15	2.1 ± 0.9 ^{a}	2.2 ± 0.8 ^{a}	0.4 ± 1.1 ^{b}	-0.2 ± 0.7 ^{b}
	JJAS 15	9.3 ± 0.5 ^{a}	8.9 ± 0.5 ^{a}	7.4 ± 1.0 ^{b}	7.0 ± 0.4 ^{b}

[1] Data in April are available from 18.04.2013

7.3 Soil moisture patterns in Rolwaling

The lowest mean pF values (corresponding to the highest soil water tension) of 0-2 were measured in summer (JJAS) and autumn (ON), while the highest pF values (corresponding to the lowest soil water tension) of 2-5 were detected in winter (DJF), followed by spring months (MAM). In the entire measurement period (01.05.2013 – 30.09.2015), NE2 was higher by pF 0.4 than NW1. On both transects, soils in the alpine tundra revealed year-round higher pF compared to lower elevations. Corresponding to higher soil temperatures in DJF 14/15 and MAM 15 than in the previous year (DJF 13/14, MAM 14), distinctly lower pF values (corresponding to higher soil water tensions) were found in DJF 14/15 and MAM 15.

A variance analysis with Post-hoc Nemenyi test of daily mean pF values (01.05.2013 – 30.09.2015) on both altitudinal transects resulted in significant differences between the zones ABC and D ($p < 0.0001$). On NW1, AB (0.38) did not vary significantly. On NE2, AB (0.82) and AD (0.34) were similar, while AC, BC, BD, and CD ($p < 0.0001$) differed significantly from each other. The same tests for daily mean soil water content and available water capacity revealed similar results.

With respect to different seasons, mean soil water contents and mean available water capacities (Table 3) mostly were significantly different between the altitudinal zones A, B, C, and D. Both transects had the year-round lowest soil water contents and available water capacities in the alpine tundra (zone D; Table 3, Fig. 6). For the entire measurement period, a decline of mean available water capacities from A to D was calculated on both transects (NE2: A = 5.53, B = 5.39, C = 5.51, D = 5.20, NW1: A = 7.13, B = 6.69, C = 5.92, D = 5.40). Likewise to pF, the highest soil water contents and available water capacities were calculated for summer (JJAS), followed by autumn (ON), spring (MAM), and winter (DJF) (Fig. 6).

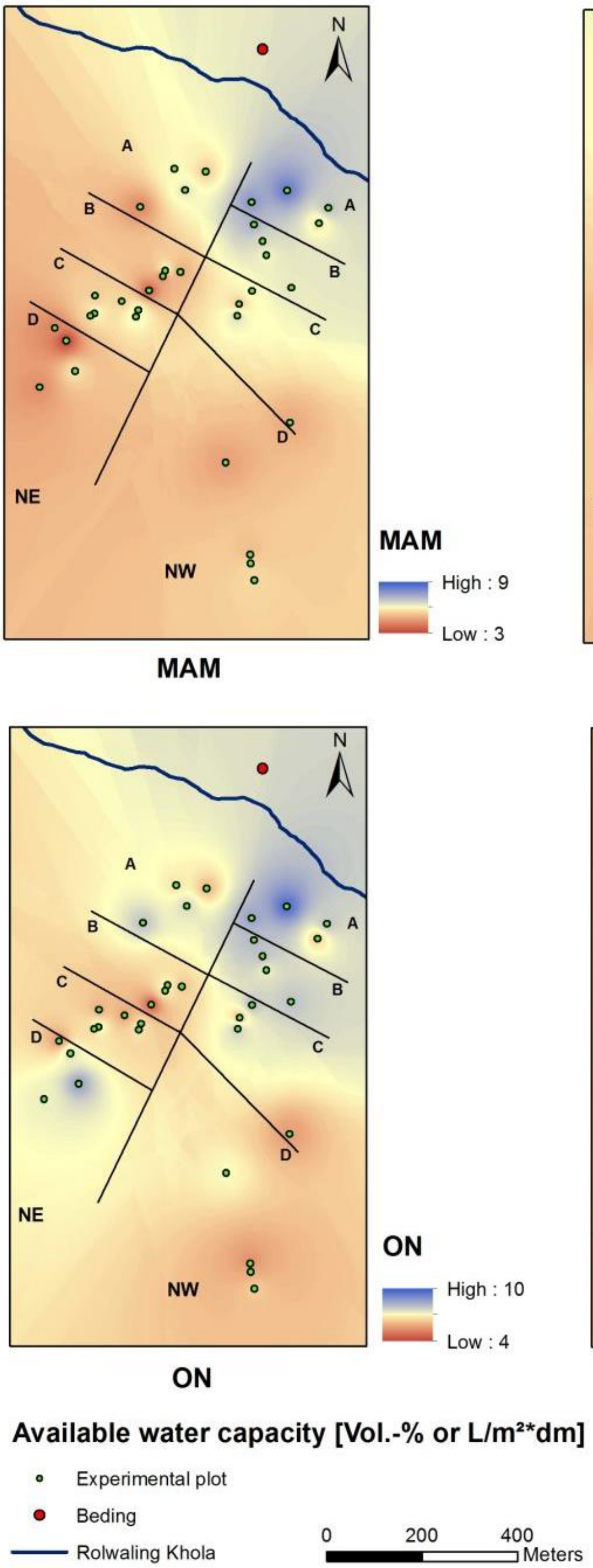

Figure 6. Spatiotemporal variation in available water capacity [Vol.-% or L $m^{-2}dm^{-1}$] at 0-10 cm soil depth. A, B, C, D = Altitudinal zones. NW = Northwest, NW1. NE = Northeast, NE2. MAM = March-May, JJAS = June-September, ON = October-November, DJF = December-February.

Table 3. Mean (± s.e.) available water capacities [Vol.-% or L m^{-2} dm^{-1}] at 10 cm soil depth in the altitudinal zones A, B, C, and D on the NE2 and NW1 transect. AM 13 = April-May 2013, JJAS = summer (June, July, August, September), ON = autumn (October, November), DJF = winter (December, January, February), MAM = spring (March, April, May). Different letters indicate significant differences at $P < 0.05$ by Post hoc Nemenyi (Tukey) test.

Transect	Season	A	B	C	D
NE2	AM 13 [1]	6.8 ± 1.3 ^{a}	6.0 ± 1.2 ^{b}	6.8 ± 0.6 ^{c}	3.6 ± 2.7 ^{d}
	JJAS 13	8.4 ± 1.8 ^{ac}	7.6 ± 1.2 ^{bc}	7.6 ± 1.1 ^{abc}	6.3 ± 1.6 ^{d}
	ON 13	6.7 ± 0.8 ^{a}	6.1 ± 2.5 ^{b}	5.8 ± 0.7 ^{c}	5.7 ± 1.8 ^{d}
	DJF 13/14	0.9 ± 1.1 ^{a}	1.7 ± 1.3 ^{a}	0.9 ± 1.1 ^{b}	0.7 ± 2.5 ^{b}
	MAM 14	4.5 ± 2.8 ^{a}	4.2 ± 1.2 ^{b}	5.2 ± 0.7 ^{b}	4.0 ± 2.0 ^{c}
	JJAS 14	7.4 ± 0.7 ^{a}	7.6 ± 1.2 ^{a}	7.4 ± 1.2 ^{a}	6.3 ± 0.6 ^{b}
	ON 14	7.7 ± 1.5 ^{a}	6.0 ± 0.5 ^{b}	6.6 ± 0.9 ^{c}	6.3 ± 1.9 ^{d}
	DJF 14/15	1.8 ± 1.8 ^{a}	3.1 ± 2.0 ^{b}	1.6 ± 0.8 ^{b}	1.2 ± 1.8 ^{a}
	MAM 15	5.7 ± 0.9 ^{a}	5.3 ± 1.6 ^{b}	5.7 ± 0.4 ^{b}	5.0 ± 1.0 ^{c}
	JJAS 15	6.9 ± 0.7 ^{a}	6.5 ± 0.8 ^{b}	7.3 ± 1.0 ^{a}	5.7 ± 0.6 ^{c}
NW1	AM 13[1]	7.8± 1.3 ^{a}	7.1 ± 0.4 ^{b}	7.0 ± 0.9 ^{c}	6.6 ± 1.0 ^{d}
	JJAS 13	8.5 ± 1. 4 ^{ab}	7.8 ± 0.7 ^{bc}	7.7 ± 1.3 ^{bc}	6.8 ± 1.0 ^{d}
	ON 13	8.0 ± 1.6 ^{a}	7.1 ± 0.2 ^{b}	6.5 ± 1.2 ^{c}	5.8 ± 0.4 ^{d}
	DJF 13/14	2.6 ± 1.9 ^{a}	1.9 ± 0.6 ^{b}	1.0 ± 1.0 ^{c}	0.3 ± 0.6 ^{d}
	MAM 14	6.8 ± 1.6 ^{a}	6.0 ± 0.2 ^{b}	5.3 ± 1.1 ^{c}	4.9 ± 0.4 ^{d}
	JJAS 14	9.0 ± 1.6 ^{a}	7.5 ± 0.6 ^{b}	8.0 ± 1.8 ^{b}	7.2 ± 1.0 ^{c}
	ON 14	8.3 ± 0.9 ^{a}	8.7 ± 1.0 ^{b}	7.3 ± 1.5 ^{c}	6.2 ± 0.9 ^{d}
	DJF 14/15	4.4 ± 2.0 ^{a}	6.4 ± 2.2 ^{a}	3.1 ± 2.1 ^{b}	3.0 ± 1.2 ^{c}
	MAM 15	7.6 ± 0.8 ^{a}	6.6 ± 1.6 ^{b}	5.9 ± 0.7 ^{c}	5.8 ± 0.7 ^{d}
	JJAS 15	8.6 ± 1.5 ^{a}	6.4 ± 1.6 ^{b}	7.3 ± 2.2 ^{c}	6.0 ± 1.0 ^{d}

[1] Data in April are available from 18.04.2013

7.4 Linking soil temperature and moisture to stand structures and tree physiognomy

In a first step, a PCA including the different soil temperature (ST) variables resulted in 70 % proportion of variance for principal component 1 (PC1) which was represented predominantly by the soil temperatures measured in the entire period (01.05.2013 – 31.10.2015), and in spring 2014 and 2015. 19 % proportion of variance was explained by principal component 2 (PC2) which included primarily spring temperatures in 2013, and winter temperatures (DJF 13/14, 14/15). The same method applied to available water capacities (AWC) revealed 50 % proportion of variance for PC1 (entire period, summer), and 31 % for PC2, mainly covered by winter and spring. A PCA of soil water content (SM) led to 40 % proportion of variance by

PC1 including the entire period, spring, and summer. PC2 (34 %) was composed primarily of winter SM.

Two different PCs (summarised as ST and AWC) were integrated as vector variables into a *Redundancy Analysis* (RDA) to test their relations to the dependent variables. Figure 7 indicates that ST is the most important independent variable on the first axis (RDA1), and that AWC is most important on the second axis (RDA2). The proportion explained by the RDA 1 axis was 99 %, while the RDA 2 axis represented 1 %. ST was strongly correlated with crown length and tree height. LAI, crown width, dbh, and the number of tree individuals correlated less strongly with both ST and AWC (Fig. 7).

The circles (Fig. 7a) indicate the different altitudinal zones. Zones A and B (closed forest, A = green, B = brown) overlap partially, whereas C (krummholz, grey), and D (alpine tundra, black) provided individual groups showing a small overlap only (confidence interval = 0.95). The groups implied a very homogeneous distribution of sites, especially the group of sites D where six sites were virtually equal (black dots in the upper left corner of Fig. 7a). With regard to exposition, no major differences occurred between the sites of the altitudinal transects NE2 and NW1 (Fig. 7b).

A summary of the RDA showed that the proportion of the total variance explained by the independent variables was 16.5 %. The *RsquareAdj* function in R was used to see the variation explained by the individual independent variables. Hereafter, the conditional effect of ST on the dependent variables was highest (6.9 %), followed by AWC (3.7 %). The shared variation of the two variables was 5.9 %. To verify these results, and to explain the effects of each independent variable on the individual dependent variables more detailed, a multivariate linear regression analysis with ensuing *MANOVA* was applied separately. The results showed that the variances of the dependent variables LAI, crown width, crown length, and tree height were best explained by ST ($p = 0.05$; see Table 4 in Manuscript 2). In summary, the model for multivariate linear regression (after *MANOVA*) was significant for ST only to predict LAI, crown width, crown length, tree height, dbh, and the number of tree individuals ($p = 0.04$).

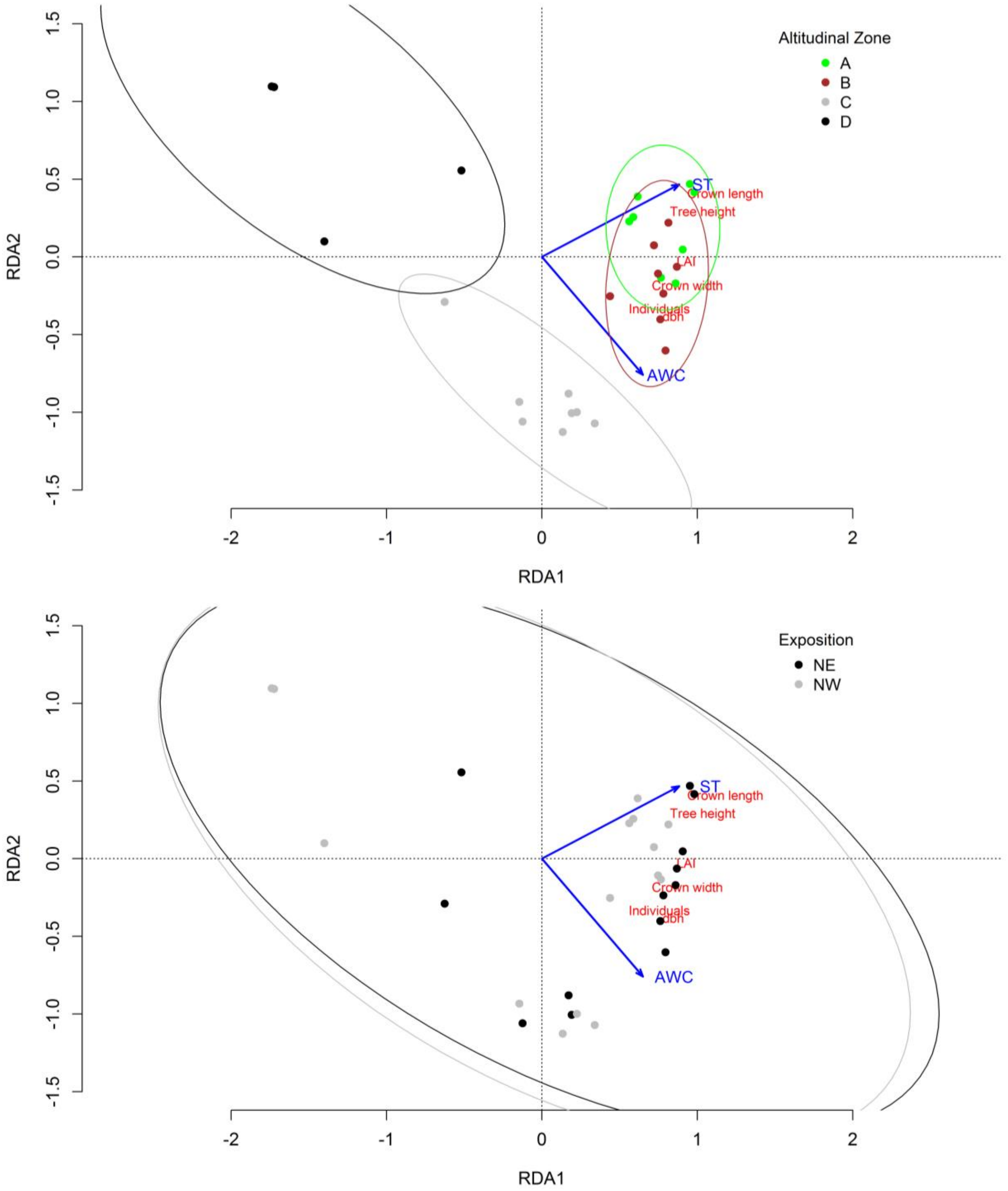

Figure 7. Results from the *Redundancy Analysis* (RDA) with regard to altitudinal zones (a), and exposition (b). Blue arrows represent the independent explanatory variables soil temperature (ST), and available water capacity (AWC) gained as best explained principal components from preceding *Principal Component Analysis* (PCA). The dependent response variables diameter in breast height (dbh), leaf area index (LAI), tree height, crown width, crown length, and number of tree individuals (Individuals) are colored in red. Circles combine related groups of sites (NE = Northeast, NE2, NW = Northwest, NW1. A, B, C, D = Altitudinal zones). Scaling = 2 (in programming language R).

In turn, the dependent variables ST, AWC, and SM together were best explained by elevation [m a.s.l.] ($p = 0.002$), and tree height ($p < 0.01$), where elevation explained 79 % of the variance in tree height. With regard to each individual dependent variable the results were similar. The model for the explanation of ST fitted best for tree height with an adjusted R^2 of the model of 13 % ($p = 0.02$). AWC was related to elevation and tree height (adj. $R^2 = 44$ %, $p < 0.001$). The results for SM looked similar, with the independent variables elevation, tree height, and number of tree individuals creating the best fitting model (adj. $R^2 = 38$ %, $p < 0.001$). Neither the soil-related independent variables (texture, bulk density, thickness of litter layer) nor aspect did improve the models.

7.5 Soil and foliar nutrient patterns in Rolwaling

7.5.1 Soil cation exchange capacity and base saturation

The concentrations of the exchangeable cations Al, Ca, Fe, K, and Mg declined with soil depth from Oe to topsoils (Ah) and Ae, enchried in Bh, and declined again in Bs (see Manuscript 4). Primarily Fe and Al accumulated in Bh. While Mn decreased almost to zero with soil depth, Na showed concentrations below the detection limit in more than half of the cases. Summarised, the cation exchange capacities (CEC, all elements included) were highest in Oe, decreased in topsoils and Ae, rised strongly in Bh, and decreased again in Bs. High base saturation was found in Oe (> 80 %), but it declined rapidly from approximately 50 % in topsoils to ca. 25 % in Ae, and ca. 10-15 % in Bh and Bs.

Some of the exchangeable cations changed along the elevational gradient and with differences in stand structures (see Appendix S2 in Manuscript 4): A significant decline with elevation [m a.s.l.] was found for K and Mg in Oe. K differed considerably between the altitudinal zones AB and CD. In contrast, Mg decreased continuously with altitudinal changes in stand structues. A similar distribution was detected for litter K and Mg. Both topsoil K and Mg were lowest in the alpine tundra, and were highest underneath krummholz. No significant correlation was found between elevation [m a.s.l.] and the exchangeable cations Al, Ca, Fe, and Mn. In summary, CEC decreased significantly with elevation [m a.s.l.] in Oe only.

7.5.2 Soil N and P availability

Plant-available soil N_{min}, and P_{av} concentrations [mg kg^{-1}] varied with altitudinal variations in stand structures (Tables 4, 5), and distinctly with soil depth (supplement of Manuscript 3). Significantly negative correlations were found between topsoil N_{min} concentrations and elevation [m a.s.l.], irrespective of the year (May 2014: r = -0.66; Sep 2014: r = -0.45; Sep 2015: r = -0.58). A one-way ANOVA resulted in significant differences of topsoil N_{min} concentrations between the subalpine forest (zones AB), and krummholz (C) and alpine tundra (D) (Table 5). Also, a significant decline in topsoil P_{av} concentrations with elevation [m a.s.l.] was found (May 2013: r = -0.46; May 2014: r = -0.61). Differences in the topsoil P_{av} concentrations among the subalpine forest (zones AB), and krummholz and alpine tundra (CD) were less pronounced (Tables 4, 5), but significant.

7.5.3 Soil C:N:P stoichiometry

The total concentrations of C, N, and P, and their ratios changed considerably with soil depth across the entire treeline ecotone. The highest total C, N, and P concentrations were found in both organic layers (Oi, Oe). In May 2013, mean soil C:N:P ratios in the study area differed significantly from 370:19:1 (topsoils) to 196:10:1 (Ae), 283:12:1 (Bh), and 221:9:1 (Bs). In the following year (May 2014), significant differences in mean soil C:N:P ratios from 457:23:1 (topsoils), 228:11:1 (Ae), 278:12:1 (Bh), and 235:9:1 (Bs) were found. Topsoil C:N ratios were remarkably consistent during all of the four sampling dates.

Significant correlations were detected between elevation [m a.s.l.] and topsoil N concentrations (May 2013: r = -0.49; May 2014: -0.63; Sep 2014: -0.60; Sep 2015: -0.65), topsoil C:N ratios (0.81; 0.64; 0.72; 0.82), and topsoil total P concentrations (May 2013: -0.49; May 2014: -0.33). For topsoil C concentrations, C:P, C:P_o, N:P, and N:P_o ratios no significant relationships with elevation [m a.s.l.] were detected. Topsoil total C and N concentrations were similar in the subalpine forest (zones AB) and krummholz (C), but were significantly different in the alpine tundra (D) at all sampling dates (Table 5). Topsoil total P concentrations varied significantly between the zones A, BC, and D (Table 4). Topsoil C:N ratios were significantly different between the zones AB and CD at all sampling dates (Table

5), while topsoil C:P and C:P_o ratios increased from the zones AB to C, but decreased significantly in D (Table 5). Topsoil N:P and N:P_o ratios were similar in the zones ABC, and differed significantly in D (Table 5). Very low N_{min}:P_{av} ratios were calculated between 0.02 and 0.1, and N_{min}:$NaHCO_3$-P_i ratios between 0.5 and 3 (Table 5). Significant differences for these ratios occurred between altitudinal zones AB and CD (Table 5).

Figure 8 shows the relationships between topsoil and litter (Oi) C:N ratios with regard to the different altitudinal zones. The relations became closer with altitudinal changes in stand structures, which were expressed by increasing coefficients of determinations from the uppermost subalpine forest (zone B; $R^2 = 0.26$), to krummholz (C; $R^2 = 0.39$), to the alpine tundra (D; $R^2 = 0.75$). In general, the thickness of the organic layer O_i decreased significantly ($r = -0.71$) with elevation [m a.s.l.], and differed significantly between ABC and D.

Table 4. Topsoil P fractions [mg kg^{-1}] in the altitudinal zones A (subalpine forest), B (uppermost subalpine forest), C (krummholz), and D (alpine tundra). Values result from a sequential Hedley P fractionation (according to Hedley et al., 1982) in May 2013 and 2014.

	Zone	**$NaHCO_3$-Pi**	**$NaHCO_3$-Po**	**NaOH-Pi**	**NaOH-Po**	**HCl-P**	**H_2SO_4-P**	**Total P**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	**Mean ± s.e.**
May 2013	A *(14)*	51.10 ± 38.47 ^{a}	155.10 ± 56.78 ^{a}	78.25 ± 25.84 ^{a}	461.38 ± 129.63 ^{a}	58.93 ± 15.74 ^{a}	45.83 ± 16.02 ^{a}	**846.33 ± 204.10 ^{a}**
	B *(12)*	69.92 ± 37.39 ^{a}	84.16 ± 33.84 ^{b}	90.29 ± 29.15 ^{a}	376.85 ± 118.32 ^{ab}	62.20 ± 16.63 ^{a}	40.70 ± 9.92 ^{a}	**724.12 ± 176.68 ^{b}**
	C *(12)*	53.92 ± 31.97 ^{a}	83.88 ± 51.07 ^{b}	60.14 ± 14.90 ^{b}	330.26 ± 82.00 ^{b}	47.96 ± 8.49 ^{a}	45.90 ± 17.82 ^{a}	**622.07 ± 110.90 ^{b}**
	D *(10)*	46.19 ± 34.22 ^{a}	94.85 ± 32.53 ^{b}	80.20 ± 32.77 ^{a}	272.87 ± 74.69 ^{b}	72.08 ± 47.38 ^{a}	29.61 ± 16.73 ^{a}	**595.80 ± 150.36 ^{c}**
May 2014	A *(14)*	60.94 ± 44.46 ^{a}	98.07 ± 33.98 ^{a}	84.23 ± 25.05 ^{a}	371.53 ± 120.42 ^{a}	58.97 ± 19.73 ^{a}	53.09 ± 35.06 ^{a}	**726.83 ± 225.00 ^{a}**
	B *(12)*	45.34 ± 32.60 ^{ab}	82.79 ± 40.60 ^{a}	70.33 ± 17.22 ^{a}	314.67 ± 74.53 ^{a}	53.27 ± 15.56 ^{a}	52.94 ± 43.48 ^{a}	**619.36 ± 179.25 ^{b}**
	C *(12)*	40.03 ± 32.56 ^{ab}	84.66 ± 48.36 ^{a}	65.11 ± 35.86 ^{a}	310.15 ± 112.05 ^{a}	43.29 ± 10.02 ^{a}	68.69 ± 32.83 ^{a}	**611.92 ± 221.32 ^{b}**
	D *(12)*	22.58 ± 15.00 ^{b}	90.59 ± 26.99 ^{a}	64.63 ± 14.19 ^{a}	313.06 ± 86.98 ^{a}	54.05 ± 17.77 ^{a}	48.57 ± 27.06 ^{a}	**593.48 ± 121.14 ^{c}**

Values are means ± standard error (s.e.); different letters between four items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.* $NaHCO_3$ = bicarbonate; SOC, NaOH = hydroxide; HCl = hydrochloric acid; H_2SO_4 = sulfuric acid; Pi = inorganic P fractions; Po = organic P fractions; P = phosphorus.

Table 5. Topsoil C, N, Pav, Po [mg g^{-1}], and Nmin [mg kg^{-1}] concentrations, and topsoil C:N, C:P, C:Po, N:P, N:Po, Nmin:Pav and Nmin:NaHCO$_3$-Pi ratios in the altitudinal zones A (subalpine forest), B (uppermost subalpine forest), C (krummholz), and D (alpine tundra) in May 2013 and 2014.

	Zone	**C [mg g^{-1}]**	**N [mg g^{-1}]**	**Nmin [mg kg^{-1}]**	**Pav [mg g^{-1}] ***	**Po [mg g^{-1}] ***	**C:N**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
May 2013	A *(14)*	204.20 ± 84.82 ^{a}	12.11 ± 5.49 ^{a}	no data	0.74 ± 0.18 ^{a}	0.62 ± 0.17 ^{a}	17.22 ± 1.15 ^{a}
	B *(12)*	235.01 ± 67.79 ^{a}	12.98 ± 3.37 ^{a}	no data	0.62 ± 0.16 ^{a}	0.46 ± 0.15 ^{b}	18.27 ± 2.59 ^{b}
	C *(12)*	245.10 ± 73.91 ^{a}	11.41 ± 3.25 ^{a}	no data	0.53 ± 0.10 ^{b}	0.41 ± 0.09 ^{b}	21.39 ± 1.59 ^{c}
	D *(10)*	171.02 ± 70.10 ^{b}	7.39 ± 3.58 ^{b}	no data	0.49 ± 0.15 ^{b}	0.37 ± 0.10 ^{b}	22.59 ± 2.37 ^{c}
May 2014	A *(14)*	240.95 ± 96.67 ^{a}	13.99 ± 5.56 ^{a}	44.70 ± 35.66 ^{a}	0.61 ± 0.18 ^{a}	0.46 ± 0.14 ^{a}	17.26 ± 1.46 ^{a}
	B *(12)*	244.36 ± 101.80 ^{a}	12.44 ± 4.66 ^{a}	46.25 ± 37.89 ^{a}	0.54 ± 0.13 ^{a}	0.40 ± 0.11 ^{b}	19.40 ± 1.77 ^{a}
	C *(12)*	274.44 ± 107.70 ^{a}	12.05 ± 4.13 ^{ab}	18.16 ± 13.70 ^{b}	0.50 ± 0.20 ^{b}	0.39 ± 0.16 ^{b}	21.52 ± 2.91 ^{b}
	D *(12)*	180.92 ± 76.27 ^{b}	8.35 ± 2.81 ^{b}	12.17 ± 7.55 ^{c}	0.48 ± 0.10 ^{b}	0.43 ± 0.11 ^{b}	21.61 ± 2.63 ^{b}

		C:P *	**C:Po ***	**N:P ***	**N:Po ***	**Nmin:Pav ***	**Nmin:NaHCO$_3$-Pi ***
May 2013	A *(14)*	286.91 ± 68.47 ^{a}	353.53 ± 108.72 ^{a}	16.90 ± 4.33 ^{ab}	20.82 ± 6.60 ^{a}	no data	no data
	B *(12)*	392.55 ± 91.32 ^{ab}	541.97 ± 134.96 ^{ab}	21.24 ± 5.44 ^{a}	29.19 ± 7.09 ^{b}	no data	no data
	C *(12)*	470.24 ± 135.92 ^{b}	620.52 ± 208.42 ^{b}	21.71 ± 5.83 ^{a}	28.67 ± 9.08 ^{b}	no data	no data
	D *(10)*	330.96 ± 131.09 ^{a}	437.93 ± 162.99 ^{a}	14.62 ± 5.58 ^{b}	19.28 ± 6.82 ^{a}	no data	no data
May 2014	A *(14)*	395.54 ± 92.21 ^{a}	520.86 ± 140.17 ^{a}	22.80 ± 4.59 ^{a}	30.02 ± 7.46 ^{a}	0.06 ± 0.04 ^{a}	0.95 ± 0.60 ^{a}
	B *(12)*	470.82 ± 131.31 ^{ab}	606.69 ± 147.13 ^{ab}	24.10 ± 5.57 ^{a}	31.23 ± 6.94 ^{a}	0.08 ± 0.04 ^{a}	1.17 ± 0.88 ^{a}
	C *(12)*	589.90 ± 256.08 ^{b}	753.25 ± 335.42 ^{b}	25.82 ± 8.28 ^{a}	32.88 ± 12.12 ^{a}	0.04 ± 0.03 ^{b}	0.66 ± 0.57 ^{b}
	D *(12)*	348.15 ± 172.26 ^{a}	427.93 ± 190.92 ^{a}	15.52 ± 5.90 ^{b}	19.13 ± 6.77 ^{b}	0.02 ± 0.01 ^{b}	0.55 ± 0.34 ^{b}

Values are means ± standard error (s.e.); different letters between four items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.* No data = no data available. *As soil component relevant for stoichiometric considerations, the sums of NaHCO$_3$- and NaOH-P-fractions (Pav), and of NaHCO$_3$- and NaOH-Po (Po), and NaHCO$_3$-Pi were used for P.

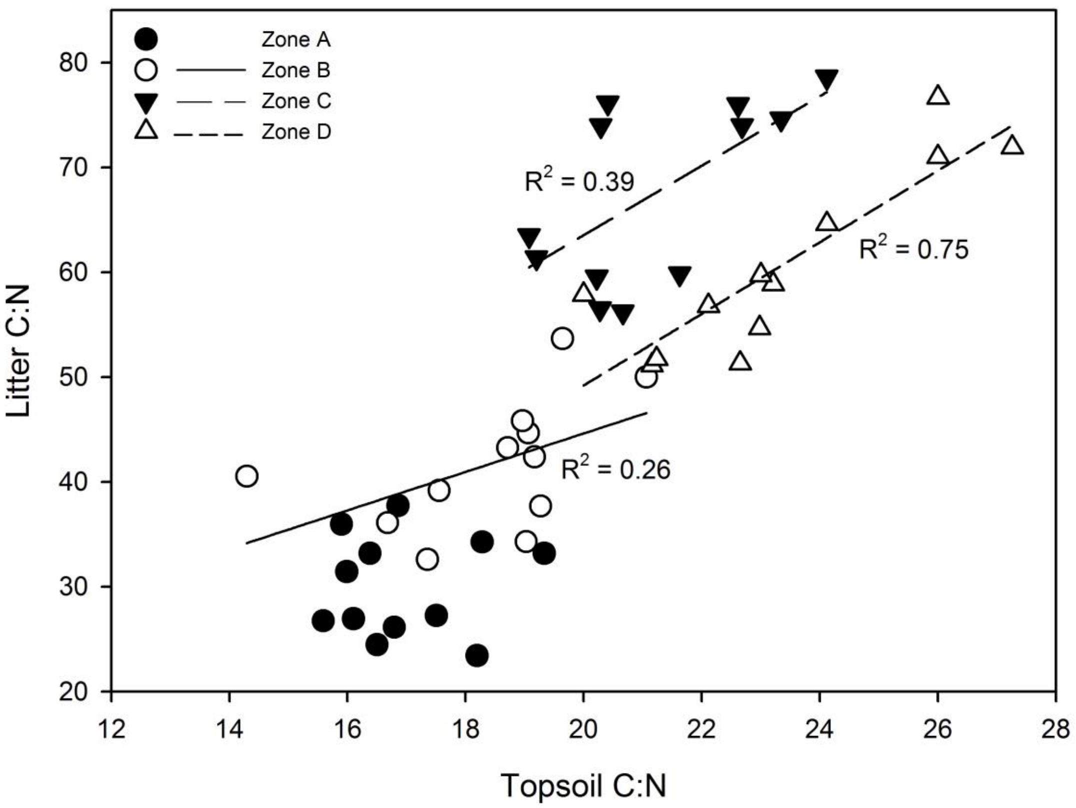

Figure 8. Relationships between topsoil (Ah) and litter (Oi) C:N ratios with respect to the altitudinal zones A (subalpine forest; filled dots), B (uppermost subalpine forest; white dots), C (krummholz; filled triangles), and D (alpine tundra; white triangles). Data originates from May 2013. Lines with R^2 indicate significant linear regressions at $P < 0.05$. No significant relationship was found in the subalpine forest (A).

7.5.4 Foliar C:N:P stoichiometry

The foliar C:N:P stoichiometric ratios were species-specific throughout the treeline ecotone. An ANOVA testing the differences between the six investigated species resulted in two different groups of species. Foliar C:N and C:P ratios in three evergreen species *Abies*, *Rhc*, and *Rhas* varied significantly from foliar C:N and C:P ratios in the three deciduous tree species *Acer*, *Betula*, and *Sorbus* (September 2014, 2015). However, the analyses did not show significant variations in foliar N:P ratios. Overall, the following mean foliar C:N:P ratios were found in the evergreen species: *Rhc* (May 2013: 433:12:1; May 2014: 404:12:1; Sep 2014: 371:14:1; Sep 2015: 381:12:1), *Abies* (414:12:1; 404:12:1; 304:12:1; 322:11:1), *Rhas* (405:12:1; 416:12:1; 442:14:1; 403:12:1). The mean foliar C:N:P ratios in the deciduous species were: *Acer* (Sep 2014: 199:12:1; Sep 2015: 206:11:1), *Betula* (234:11:1; 226:12:1), *Sorbus* (230:9:1; 281:11:1).

Furthermore, foliar C:N:P stoichiometry varied with altitudinal changes in stand structures (Table 6; supplement Manuscript 3). Likewise, the six investigated species showed diverse trends in foliar nutrient concentrations with elevation [m a.s.l.] (Fig. 9). Foliar C concentrations in the evergreen species *Abies*, *Rhc*, and *Rhc* were not significantly related to elevation [m a.s.l.] nor did they differ between the altitudinal zones (Table 6). Foliar C concentrations in deciduous *Sorbus* increased significantly with elevation [m a.s.l.] (Fig. 9), and also differed significantly between the subalpine forest (zones AB), and krummholz and the alpine tundra (CD). In deciduous *Acer*, foliar C concentrations decreased significantly with elevation [m a.s.l.] (Fig. 9), and also varied significantly between the zones AB and C in September 2015.

Foliar N concentrations decreased significantly with elevation [m a.s.l.], except for *Abies*, and for *Betula* in September 2015 (Fig. 9). In *Rhc* (Table 5), a significant decrease of foliar N concentrations with elevation [m a.s.l.] was determined at all sampling dates (May 2013: r = -0.76; May 2014: -0.67; Sep 2014: -0.69; Sep 2015: -0.77). Referred to altitudinal zones, an abrupt significant decline in foliar N concentrations (*Rhc*) occurred in particular at the transitions from B to C (May 2013, 2014), and from C to D (Sep 2014, 2015; Table 6). For the other species, significant differences were found between ABC and D (*Abies*), AB and CD (*Sorbus*), AB and C (*Betula*), and C and D (*Rhas*). The deciduous species *Acer*, *Betula*, and *Sorbus* had significantly higher foliar N concentrations compared to the evergreen species *Abies*, *Rhc*, and *Rhas* (resulting from a one-way ANOVA).

Foliar P concentrations decreased significantly with elevation [m a.s.l.] in *Acer*, *Rhc*, and *Sorbus*, but not in *Abies*, *Betula*, and not in May 2014 and September 2014 in *Rhas*. The strongest significantly negative correlations with elevation [m a.s.l.] were detected in *Rhc* (May 2013: r = -0.50; May 2014: -0.62; Sep 2014: -0.43; Sep 2015: -0.62) (Fig. 9). A one-way ANOVA resulted in significant differences in *Abies* foliar P concentrations between the altitudinal zones ABC and D, and AB and CD (May 2014). In *Acer*, *Rhc*, and *Sorbus*, foliar P concentrations dropped from B to C, and most notably at the transition from C to D (Table 6).

In *Rhas*, foliar P concentrations were different between C and D in May 2013 and September 2015. The deciduous species had significantly higher foliar P concentrations than the evergreen species (one-way ANOVA).

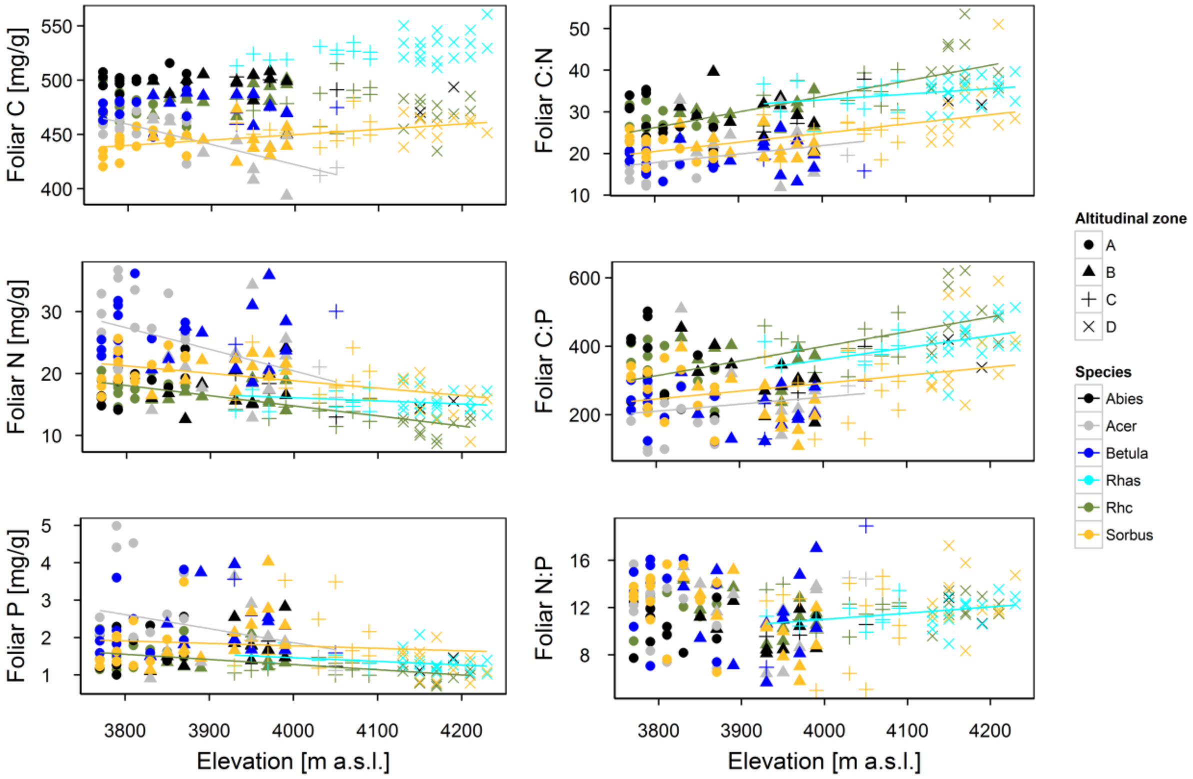

Figure 9. Changes in foliar C, N, and P concentrations [mg g^{-1}], and foliar C:N, C:P, and N:P ratios along the elevational gradient [m a.s.l.], and with regard to the different altitudinal zones A, B, C, D. Data originates from September 2015. Lines indicate significant linear regressions at $P < 0.05$. The graphs include the tree and shrub species *Abies spectabilis* (Abies), *Acer caudatum* (Acer), *Betula utilis* (Betula), *Rhododendron campanulatum* (Rhc), *Rhododendron anthopogon/setosum* (Rhas), and *Sorbus microphylla* (Sorbus). Three tree species only (Abies, Rhc, Sorbus) occur in all altitudinal zones (A, B, C, D).

Significantly positive correlations were found between foliar C:N ratios and elevation [m a.s.l.] in *Rhc*, *Sorbus*, *Rhas* (May 2013, Sep 2015), *Betula* (Sep 2014), and *Acer* (Sep 2015) (Fig. 9). The most remarkable significant increase in foliar C:N ratios showed *Rhc* (May 2013: r = 0.77; May 2014: 0.71; Sep 2014: 0.65; Sep 2015: 0.79; Table 6) and *Sorbus* (Sep 2014: 0.71; Sep 2015: 0.50). Foliar C:N ratios differed significantly between the subalpine forest (zones AB), krummholz (C), and the alpine tundra (D) in *Rhc* (Table 6) and *Sorbus*. In

Abies, zone D varied significantly from zones ABC. Foliar C:N ratios in *Acer* were significantly different between zones A and BC.

Foliar C:P ratios increased significantly with elevation [m a.s.l.] in *Rhc*, *Sorbus*, *Rhas* (May 2013, Sep 2015), and *Acer* (Sep 2015) (Fig. 9). The increase was observed especially in *Rhc* (May 2013: 0.51; May 2014: 0.48; Sep 2014: 0.57; Sep 2015: 0.59). The stoichiometric ratios of C and P varied significantly between the subalpine forest (zones AB), and krummholz (C) and tundra (D), respectively, in *Rhc* (Table 6), *Abies*, and *Sorbus*.

In contrast to C:N and C:P, the N:P ratios in each species were relatively constant with elevation [m a.s.l.], and usually did not change significantly between the altitudinal zones.

7.5.5 Foliar nutrients K, Mg, and Mn

Apart from foliar C, N and P, significantly negative correlations with elevation [m a.s.l.] were determined for foliar K, while foliar Mg showed a weak to moderate, but also significant relationship (species: *Rhc*) (see Manuscript 4). Foliar K was similar in the subalpine forest (zones A and B), but significantly higher compared to krummholz (C) and the alpine tundra (D). Foliar Mn was extraordinarily high in D, however with high standard deviations. The same spatial patterns were determined for *Abies*, however, with considerably lower Mn.

Table 6. Foliar C, N and P concentrations, and foliar C:N, C:P and N:P ratios in *Rhododendron campanulatum* in the altitudinal zones A (subalpine forest), B (uppermost subalpine forest), C (krummholz), and D (alpine tundra). Sampling took place in four field campaigns (May 2013, 2014; September 2014, 2015).

	Zone	**C [mg g^{-1}]**	**N [mg g^{-1}]**	**P [mg g^{-1}]**	**C:N**	**C:P**	**N:P**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
May 2013	A *(11)*	474.99 ± 5.49 ^{a}	15.62 ± 1.71 ^{a}	1.33 ± 0.27 ^{a}	30.71 ± 3.12 ^{a}	371.95 ± 77.05 ^{a}	12.07 ± 1.82 ^{a}
	B *(12)*	477.91 ± 4.96 ^{a}	15.09 ± 1.19 ^{a}	1.28 ± 0.27 ^{a}	31.85 ± 2.42 ^{a}	389.44 ± 76.53 ^{a}	12.13 ± 1.63 ^{a}
	C *(19)*	481.42 ± 5.40 ^{a}	12.66 ± 1.36 ^{b}	1.13 ± 0.23 ^{a}	38.46 ± 4.18 ^{b}	443.67 ± 87.73 ^{b}	11.64 ± 1.71 ^{a}
	D *(13)*	483.33 ± 16.35 ^{a}	11.13 ± 0.95 ^{c}	0.95 ± 0.13 ^{b}	43.69 ± 3.59 ^{c}	518.24 ± 83.49 ^{b}	11.91 ± 1.54 ^{a}
May 2014	A *(18)*	467.62 ± 12.38 ^{a}	16.19 ± 1.00 ^{a}	1.30 ± 0.12 ^{a}	28.98 ± 1.84 ^{a}	363.68 ± 34.09 ^{a}	12.56 ± 0.97 ^{a}
	B *(15)*	461.76 ± 16.20 ^{a}	15.70 ± 1.83 ^{a}	1.28 ± 0.23 ^{a}	29.79 ± 3.69 ^{a}	372.68 ± 77.58 ^{a}	12.48 ± 1.74 ^{a}
	C *(20)*	454.74 ± 26.30 ^{ab}	13.51 ± 1.89 ^{b}	1.08 ± 0.22 ^{b}	34.16 ± 4.12 ^{b}	433.49 ± 72.51 ^{b}	12.78 ± 2.11 ^{a}
	D *(12)*	470.76 ± 22.70 ^{ac}	12.24 ± 1.60 ^{b}	1.05 ± 0.15 ^{b}	38.81 ± 3.17 ^{c}	454.28 ± 50.91 ^{b}	11.70 ± 0.82 ^{a}
Sep 2014	A *(14)*	470.24 ± 15.69 ^{a}	20.30 ± 5.47 ^{a}	1.42 ± 0.26 ^{a}	24.72 ± 6.33 ^{a}	342.49 ± 65.65 ^{a}	14.74 ± 4.86 ^{a}
	B *(12)*	467.14 ± 25.71 ^{a}	19.58 ± 5.78 ^{a}	1.37 ± 0.20 ^{ab}	26.15 ± 8.57 ^{a}	351.06 ± 71.38 ^{a}	14.43 ± 4.00 ^{a}
	C *(12)*	467.80 ± 24.02 ^{a}	19.28 ± 4.70 ^{a}	1.33 ± 0.29 ^{ab}	25.93 ± 7.60 ^{a}	362.27 ± 57.92 ^{a}	15.03 ± 4.53 ^{a}
	D *(10)*	496.87 ± 45.51 ^{a}	14.40 ± 5.24 ^{b}	1.13 ± 0.14 ^{b}	36.90 ± 7.65 ^{b}	444.30 ± 56.61 ^{b}	12.87 ± 4.68 ^{a}
Sep 2015	A *(14)*	477.15 ± 11.25 ^{a}	18.05 ± 2.19 ^{a}	1.55 ± 0.34 ^{a}	26.81 ± 3.33 ^{a}	320.76 ± 67.47 ^{a}	11.87 ± 1.34 ^{a}
	B *(12)*	478.22 ± 26.02 ^{a}	18.16 ± 5.31 ^{a}	1.48 ± 0.33 ^{a}	27.84 ± 5.76 ^{a}	321.65 ± 96.80 ^{a}	11.33 ± 2.12 ^{a}
	C *(12)*	481.34 ± 16.75 ^{a}	14.19 ± 1.43 ^{a}	1.22 ± 0.17 ^{b}	34.21 ± 3.33 ^{b}	402.25 ± 54.53 ^{b}	11.78 ± 1.31 ^{a}
	D *(11)*	469.84 ± 14.73 ^{a}	11.44 ± 1.51 ^{b}	0.97 ± 0.19 ^{c}	41.70 ± 5.52 ^{c}	500.66 ± 91.46 ^{c}	11.96 ± 1.10 ^{a}

Values are means ± s.e.; different letters between two items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.*

7.5.6 Linking soil and foliar C:N:P stoichiometry

Using bivariate linear regression analyses, the relationships between topsoil C:N and foliar C:N ratios were tested (Fig. 10) which were significant for *Rhc* (May 2013: $R^2 = 0.57$; May 2014: $R^2 = 0.48$; Sep 2014: $R^2 = 0.38$; Sep 2015: $R^2 = 0.56$). With respect to altitudinal zones, the linear regressions were significant in B (May 2013), C (May 2014, Sep 2014, 2015), and D (May 2014). Significant C:N relationships were also found for *Abies* (Sep 2014: $R^2 = 0.17$), *Sorbus* (Sep 2014: $R^2 = 0.18$), and *Acer* (Sep 2015: $R^2 = 0.12$).

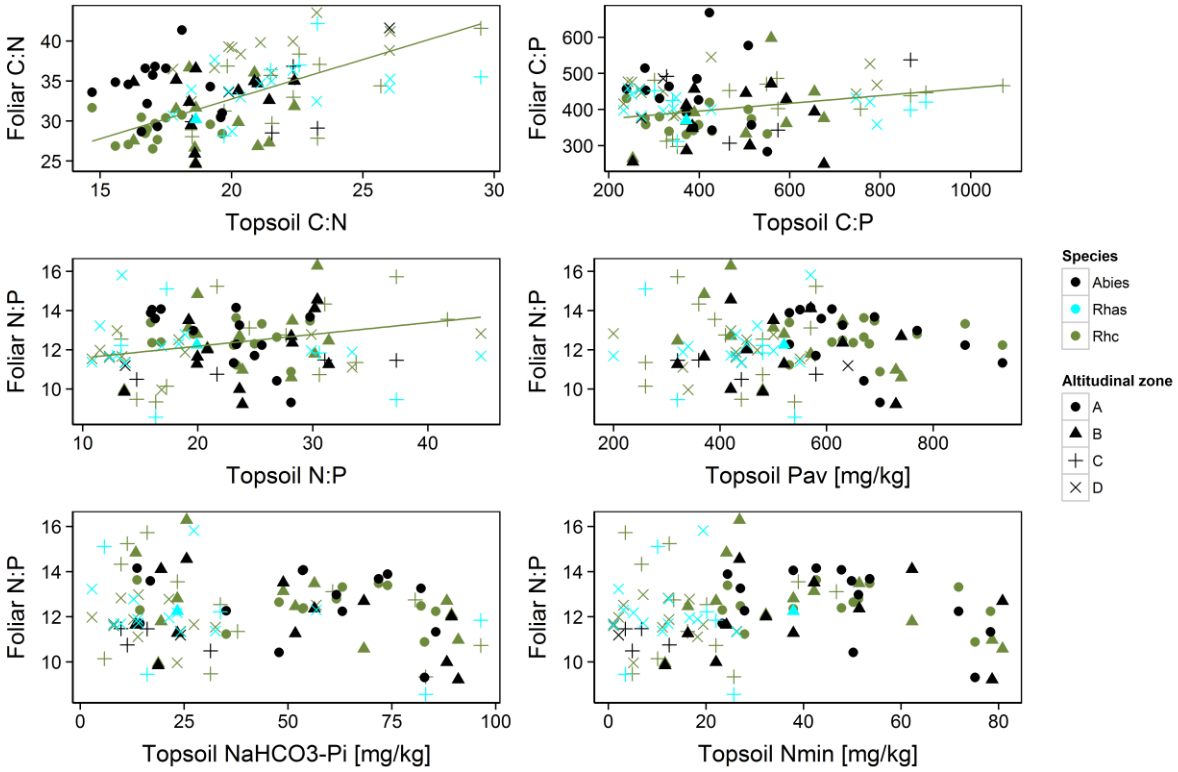

Figure 10. Relationships between topsoil C:N, C:P, N:P ratios and foliar C:N, C:P, N:P ratios, and between topsoil P_{av}, $NaHCO_3$-P_i, N_{min} concentrations [mg kg^{-1}] and foliar N:P ratios for the species *Abies spectabilis* (Abies), *Rhododendron anthopogon/setosum* (Rhas) and *Rhododendron campanulatum* (Rhc). Data originates from May 2014. Lines indicate significant linear regressions at $P < 0.05$.

The same tests for C:P ratios resulted in a significant but weak relation for *Abies* (May 2013: $R^2 = 0.07$) and *Rhc* (May 2014: $R^2 = 0.18$; Fig. 10). *Rhc* showed a significant relation between foliar N:P and topsoil N:P ratios (May 2014: $R^2 = 0.14$; Fig. 10). Furthermore, linear regressions were tested between topsoil P_{av} and foliar N:P ratios which were significant for

Rhas in May 2013 only (R^2 = 0.29). The relationships between topsoil N_{min} and foliar N:P ratios were significant for *Abies* (0.13), *Rhas* (0.11), and *Acer* (0.20) in September 2015. No significant relationships among topsoil $NaHCO_3$-P_i and foliar N:P ratios was found (Fig. 10). Multiple linear regression analyses used for testing the relations between the foliar nutrients in each species individually, and soil nutrient availability and soil C:N:P stoichiometry revealed diverse results (Table 7). Foliar C:N and C:P ratios in *Rhc* were predominantly related to topsoil C:N ratios. The other species showed more complex relationships, and especially for the deciduous tree species (e.g. *Betula*) the relations were often not significant (Table 7).

Table 7. Multiple linear regression analyses for comparison of the relationships between foliar C:N:P stoichiometry in each species (*Rhc, Rhas, Abies, Acer, Betula, Sorbus*), and topsoil nutrient availability (N_{min}, P_{av}) and C:N:P stoichiometry.

	Foliar	***Rhc***	***Rhas***	***Abies***
May 2013	C:N	C:N***, N:P* (0.60, ***)	C***, C:N* (0.60, ***)	-
	C:P	N**, C:N* (0.34, ***)	-	C:P* (0.07, *)
	N:P	-	Pav** (0.29, **)	-
May 2014	C:N	C:N*** (0.48, ***)	Pav**, C:P**, Nmin** (0.52, **)	-
	C:P	C:N*, Nmin* (0.21, **)	-	-
	N:P	C:N*, C:P* (0.11, *)	N**, C*, C:N* (0.37, *)	C*, N*, C:P* (0.24, *)
Sep 2014 [2]	C:N	C:N*** (0.38, ***)	C:N* (0.13, *)	C:N**, C*, N* (0.22, *)
	C:P	C:N** (0.14, **)	N*, C* (0.24, *)	-
	N:P	C**, Nmin*, C:N* (0.13, *)	-	C**, N* (0.23, *)
Sep 2015 [2]	C:N	C:N***, C*** (0.72, ***)	-	-
	C:P	C:N***, C*** (0.48, ***)	-	Nmin* (0.14, *)
	N:P	-	Nmin* (0.11, *)	Nmin* (0.13, *)
		Acer **[a]**	***Betula*** **[a]**	***Sorbus*** **[a]**
Sep 2014 [b]	C:N	-	-	C:N** (0.18, **)
	C:P	-	-	-
	N:P	-	-	-
Sep 2015 [b]	C:N	C:N* (0.12, *)	-	N*** (0.31, ***)
	C:P	Nmin* (0.18, *)	-	Nmin* (0.12, *)
	N:P	Nmin* (0.20, *)	C** (0.19, **)	-

Statistical significance at $P < 0.001$***, $P < 0.01$**, and $P < 0.05$* (multiple linear regression analyses). R^2 and *P* (as *, **, ***) of the linear models are shown *in parentheses.* "-" means that no significant model was achieved. [a] In May 2013 and 2014, the deciduous tree species *Acer*, *Betula*, and *Sorbus* were not sampled (no leaves developed during field campaigns). [b] In September 2014 and 2015, Hedley soil P was not measured.

8 Discussion

In a first step, this thesis reviewed the diverse alpine treeline-related literature. The review showed that especially soil nutrient and moisture patterns in alpine treeline ecotones are barely explored, and that some regions have not gained adequate attention yet. In a second step, this thesis showed that in the framework of the extensive case study in Rolwaling low soil nutrient and moisture availability, and pedogenic features in general (podzolisation) may override a low soil temperature limitation of tree growth at its upper limit at a local scale. This assumption is strengthened by year-round warmer soil temperatures in the alpine tundra than in the subalpine forests and krummholz below, at least at NE exposition. This thesis suggests a complex interaction of different factors (soil temperature, soil moisture availability, snow cover, wind, topography-induced solar radiation, vegetation, soil nutrient availability) to constrain tree growth and tree recruitment in Rolwaling.

8.1 Effects of soil properties on alpine treelines (Manuscript 1)

The analyses of 507 alpine treeline-related studies revealed that soil properties were considered in different ways and intensities. Soil temperature was found to be the factor with the second highest relative importance for tree growth at its upper limit after air temperature, both at global and local scales (Fig. 3a). This result can be strengthened by the fact that soil temperatures have possible direct effects on tree growth. A main issue in 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 was among the most discussed factors, was supposed to have the fourth highest relative importance for tree growth, however greater at a local than at a global scale (Fig. 3a), and was found to vary greatly between the different ecozones (Fig. 3b). A main issue in this point is that soil moisture conditions in alpine treeline ecotones in general have barely been measured or investigated more profoundly. Thus, their effects on tree growth have rarely been quantified, and were rather descriptive. Soil and foliar nutrients are underrepresented in literature (Fig. 3a). This suggests that nutrients are less important for tree growth under extreme conditions. Many recent findings not related to alpine treelines show the dominant importance of soil nutrients, e.g. P (e.g. Wang et al., 2011; Bergh et al., 2014; Kanzler et al., 2015), and the results of this thesis might reflect the fact that the scientific understanding is constantly evolving. This awareness also concerns other factors such as soil physical properties (e.g. soil texture, soil organic matter quality) and C balance / limitation (Fig. 3a). For instance, 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. Other factors that influence acquiring and recycling of nutrients in soils like mineral weathering, frost-thaw-cycling (permafrost-affected soils), soil microorganisms, and mycorrhizal funghi were detected highly underrepresented in treeline literature.

Major differences were found in the relevance of soil properties for tree growth in different ecozones (Fig. 3b). 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 (Fig. 3b). 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 (Fig. 3b). 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.

In general, the literature review showed different results amongst many authors with regard to the relative importance of treeline-controlling factors. Independent from single factors, contrasts in valuation were often related to the scale type (Fig. 3a) and the ecozones (Fig. 3b) where the research was conducted. In addition, previous treeline literature may be dominated by a few researchers, which might face a bias problem. Therefore, quantitative and experimental research is urgently needed. 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. This sort of hierarchy of factors should account for this type of thinking around treeline-controlling factors presented in the literature review.

8.2 Interactions among soil properties and variations in stand structures in Rolwaling (Manuscripts 1-5; Book chapter)

8.2.1 Soil temperature patterns in Rolwaling

Multivariate statistical analyses implied a significant interaction between soil temperatures, and variations in stand structures and tree physiognomy. In fact, soil temperatures indicated a significant decline with elevation [m a.s.l.], and hereby especially at the transition from the uppermost subalpine forest (B) to krummholz (C) (equal to timberline and treeline in this case). The reason, why the statistical analyses did not result in a significant relation between soil temperatures and elevation [m a.s.l.] on NE2 is due to year-round higher soil temperatures in the alpine tundra (D) compared to krummholz (Fig. 5). This suggests a stronger influence of solar radiation in this area, and points to the effect of dense canopies preventing soil heat flux and radiative warming particularly underneath krummholz (cf. Aulitzky, 1961; Körner, 1998a, b; Körner and Paulsen, 2004). Differences in the canopy cover were confirmed by substantially higher LAI values in the krummholz zone (C) than in the alpine tundra (D). This holds also true for NW1, where the canopy was generally less dense (lower LAI) compared to NE2 along the entire transect (see Manuscript 2). However, soil temperature patterns were different on NW1 with the generally lowest soil temperatures in the alpine tundra compared to lower elevations throughout the entire measurement period, except for autumn 2013 and winter 2013/14. Despite a less dense canopy on NW1, less influence of solar radiation is suggested here than on NE2.

Since mean soil temperatures at treeline during the growing seasons in 2013, 2014, and 2015 were slightly higher or same on NW1 than on NE2 (Fig. 4), and the treeline is located approximately 100 m lower in elevation, it is assumed that soil temperatures alone are not responsible for the altitudinal position of the treeline in the study area. Moreover, the higher growing season mean soil temperature at treeline of 7.5 ± 0.6°C compared to a suggested global mean of 6.4 ± 0.7°C (Körner, 2012) may indicate that a combination of different factors (e.g. soil moisture availability, soil nutrient availability; see 8.2.2 and 8.2.4) limits tree growth before temperature does (e.g. Leuschner, 1996; Harsch and Bader, 2011). Harsch and

Bader (2011) suggest that warmer treelines are governed by seedling survival rather than growth, since seedlings are said to depend strongly on water and nutrient availability, frost damage, or are intolerant to sun exposure (e.g. Ball et al., 1991; Germino et al., 2002; Gieger and Leuschner, 2004; Holtmeier and Broll, 2007).

However, the approximately 100 m higher position of the altitudinal zones in combination with the higher mean soil temperatures in the alpine tundra on NE2 suggest that tree recruitment and growth are favored depending on a topography-induced higher solar radiation load. Nevertheless, the causes for this shift remain uncertain, since mean soil temperatures underneath the subalpine forest and krummholz were similar or the same than on NW1, and thus the differences in the present distribution of subalpine forest and krummholz with regard to exposition cannot be explained by the current soil temperature patterns. The higher soil temperatures in the alpine tundra on NE2 may be responsible for a benefit in seedling establishment, and thus tree recruitment. However, the number of seedlings and saplings counted was remarkably higher in the alpine tundra on NW1 (see Manuscript 5), and seedling establishment may be overridden by poor soil moisture conditions (see 8.2.2). The similar soil temperatures underneath subalpine forest and krummholz on NE2 and NW1 may also be the reason why exposition as independent variable did not explain soil temperature patterns in the statistical analyses. Also, simple linear regression analyses did not show major differences in the relationships between soil temperatures, and relevant vegetation variables (tree height, crown length) with regard to exposition.

Overall, the results reveal a complex microclimatic pattern of soil temperatures, which may be caused by topography-induced higher solar radiation load, and thus differences in soil temperatures in the alpine tundra, and also by the stand structures themselves, which influence soil climatic conditions inside and outside of the subalpine forest and krummholz in different ways by shading effects and variation in leaf fall. Using the growing season mean soil temperature of 6.4 ± 0.7°C (Körner, 2012) as a predictor for treeline position, the treeline in Rolwaling would be located 500 to 600 m higher in elevation. This result questions 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; see Manuscript 5 and Book chapter).

8.2.2 Soil moisture patterns in Rolwaling

Multivariate statistical analyses did not show a significant impact of soil available water capacity (0-10 cm soil depth) on stand structures and tree physiognomy. In turn, soil water content and available water capacity were likely controlled by tree height and elevation [m a.s.l.], and available water capacity was additionally related to the number of tree individuals. Since elevation / altitude as environmental variables cannot explain differences in soil moisture (Körner, 2012), less importance was attached to elevation [m a.s.l.] as an explanatory variable.

On both NE2 and NW1 transects, the year-round lowest available water capacities in the alpine tundra (D; Fig. 6) are most likely critical in preventing seedlings from invading such sites. This assumption also comes from the result that the abundance of young growth from species *Abies*, *Betula*, and *Rhc* over almost all size classes was significantly correlated to soil moisture in the entire study area, and was lowest in the alpine tundra (see Manuscript 5). Thus, seedling establishment in early life stages, especially in the alpine tundra, is assumed to be likely modified by soil moisture availability, and to depend on protection from excessive solar radiation by other small growing plants (dwarf shrubs), and by topographical shelters (e.g. large rocks). The same was found for the regeneration of *Betula* (Shrestha et al., 2007), and *Abies* (Ghimire and Lekhak, 2007) in the Manang Valley, Himalaya, where *Abies* seedling abundance has been observed to depend additionally on soil P availability. Limited soil moisture supply was discussed to affect nutrient uptake by plants at other treelines (Loomis et al., 2006; Macek et al., 2012).

The main reasons for generally low water-holding capacities of soils in the study area are rapidly draining sandy substrates, low bulk densities (~ 1 g cm^{-3}), and a large amount of skeleton (up to 95 %), and thus a pronounced water percolation from the topsoils to the subsoils. In the alpine tundra, soil moisture conditions, and also water potential in plants are additionally affected by evapotranspiration provoked by a stronger influence of solar radiation and wind compared to forest (B) and krummholz (C) sites, resulting in an enhanced drying of topsoils and plants. Compared to forest sites, desiccation of topsoils through solar radiation and wind is strengthened by a less developed organic layer (litter layer < 0.5 cm) (cf. Wardle, 1968; Doležal and Šrutek, 2002). Likewise, tree regeneration has been observed being strongly hindered by water stress and excessive solar radiation at treelines worldwide (e.g. Aulitzky, 1960, 1961; Ferrar et al., 1988; Bader et al., 2007; Gill et al. 2015; Moyes et al., 2015; Piper et al., 2016).

8.2.3 Interactions between soil temperature and soil moisture

Soil moisture conditions were affected by low soil temperatures indirectly through freezing of soil water, predominantly in winter and spring. Soils across the alpine treeline ecotone were frozen from end of October 2013 at least until end of April 2014. Higher soil temperatures (around 0°C), and higher soil moisture and available water capacities in winter 2014/15 and spring 2015 compared to the same seasons in the previous year suggest a thicker snow pack during these seasons (see Manuscript 2). This conclusion derived from findings that a greater snow depth usually induces warmer soils (Holtmeier and Broll, 2007, 2010; Wieser and Tausz, 2007), leading to consistent soil temperatures around 0°C (Green, 1983; Stöhr, 2007; Shi et al., 2008; Holtmeier, 2009). Additionally, a thicker snow cover usually leads to higher soil moisture during winter, and protects soils and small plants (dwarf shrubs and seedlings) from cold temperatures, evapotranspiration, and damage by high solar radiation and wind (Holtmeier, 2009). In the Ural Mountains, warmer soils due to a thick snow cover were found to be more important for tree growth and treeline advance than summer temperatures (Hagedorn et al., 2014). In turn, a missing or thin snow cover may induce deep soil freezing (Wieser and Tausz, 2007). Thus, frost drought due to frozen soils, and mechanical damage, have been assumed to be limiting for tree growth, especially during winter months, when water uptake by plants is impeded (e.g. Kupfer and Cairns, 1996; Mayr et al., 2006; Kullman, 2007). The issue of frost drought in the study area is supported by the data from winter 2013/14, and partly spring 2014 (March, April), when both soil temperatures (< 0°C) and soil moisture were low. In contrast, winter desiccation has been negated as a cause for treeline formation (e.g. Slatyer, 1976; Körner, 1998a; Richardson and Friedland, 2009). However, late winter, and in particular spring water losses were observed not being replaced due to frozen soils and stem bases (Körner, 1998a), leading to damage of leaves / needles and branches. In the study area, winter and pre-monsoonal drought stress –in case a sufficient snow cover is missing- may not only be a problem under canopies but also in the alpine tundra, resulting in impeded tree growth and regeneration. This has been observed for several other Himalayan treelines (see Manuscript 5). In contrast to frost drought stress, it has been suggested that constraints on tree growth due to warming-related drought stress may nullify any beneficial effect on alpine treelines due to rising temperatures in the context of climate warming (González de Andrés et al., 2015).

The results showed that monitoring and analysing spatiotemporal soil temperature and soil moisture data over a longer period of time is valuable for a distinction of soil temperature and soil moisture patterns between different topographic settings, different seasons, and different years. Considering soil temperature and soil moisture conditions during growing season only is insufficient to understand the complex mechanisms determining the interactions between soil temperatures as well as soil moisture, and topography and stand structures in an alpine treeline ecotone at a local scale.

8.2.4 Soil nutrient patterns in Rolwaling

Generally complex spatiotemporal patterns of soil nutrient availability, and soil C:N:P ratios were found in the Rolwaling treeline ecotone.

First, soil plant-available N_{min} and P_{av} concentrations as well as soil C:N:P ratios varied significantly with soil depth (see Manuscript 3), and were associated with an intense podzolization favored by precipitation sums of higher than 1000 mm a^{-1}, especially during the summer monsoon. This results in an outwash of SOM (C in this case), organic acids, total and plant-available N and P, and Ca, K and Mg concentrations from topsoils to subsoils. Podzolisation is a common process occurring from the upper montane belt to the treeline in the Himalaya (Bäumler, 2015). Apart from the organic layers Oi and Oe, the highest mean soil C:N:P ratios occurred in topsoils. The fact, that soil nutrients declined considerably with soil depth, and that the investigated species are prevailing shallow-rooting trees, suggests that the vertical transport of nutrients and potentially mineralisable SOM is a general problem in the study area impeding growing conditions for trees. These assumptions are likely, because Podzols usually feature a scarcity of N, P, and also K availability. Moreover, nutrient availability (esp. P) is generally limited by low soil pH (from 2.5 to 4), since under acidic conditions the availability of P commonly decreases due to precipitation of phosphate ions together with Al and Fe (Cross and Schlesinger, 1995; Khanna et al., 2007). A high contribution of organic P fractions (biologically derived P_o) to total soil P concentrations was ascertained (Table 4), which is a function of soil development in highly weathered soils (Cross and Schlesinger, 1995). Under such conditions, also P_o is fixed in metal-organic complexes.

Second, plant-available soil nutrient concentrations and soil C:N:P ratios differed with altitudinal variations in stand structures. According to that, the results suggest different nutrient dynamics in the alpine tundra (zone D) as compared to the subalpine forest (A), the uppermost subalpine forest (B), and krummholz (C). Wider topsoil C:N ratios with elevation suggest that decomposition of SOM decreases as a result of decreasing soil temperatures or soil moisture (cf. Bäumler, 2015). Lower soil moisture availability in the alpine tundra (see 8.2.2) can decrease the accessibility of nutrients, hamper microbial activity, and consequently, induce N and P immobilisation in microbial biomass and plants (Aponte et al., 2010). The wider C:N ratios in the alpine tundra, however, did not derive from the highest but the lowest topsoil C concentrations and even lower N concentrations. Moreover, the lowest topsoil C concentrations led to a significant decline of C:P and C:P_o ratios in the alpine tundra despite significantly lower P and P_o concentrations. The lowest topsoil C concentrations in the alpine tundra are likely the result of a very low input of litter (thickness < 0.5 cm; see 7.5.3) from the dominant evergreen dwarf shrub species *Rhas* into soils. Nevertheless, in combination with a decrease in mineralisation of a thin litter layer as it is suggested by closer relationships between soil C:N and litter C:N (Fig. 8), and soil C:P and litter C:P with elevation, this resulted in a low accumulation of SOM in alpine tundra soils. Additionally, a lower decomposition at higher elevations includes less mineralisation of N and P, and thus lower soil N and P availability. However, significantly closer topsoil N_{min}:P_{av} and N_{min}:$NaHCO_3$-P_i ratios with elevation (Table 5) are rather caused by a stronger decline in topsoil N availability than P availability. Topsoil N:P_o ratios should remain constant since N and P_o are both governed by mineralisation. However, again a stronger decrease in N relative to P_o in the alpine tundra (zone D) resulted in significantly lower N:P_o ratios in this area which is again likely caused by a very low litter input and less mineralisation compared to the subalpine forest (AB) and krummholz (C). In krummholz (C), the highest topsoil C:P ratios and C concentrations occurred as compared to the subalpine forest (AB) and the alpine tundra (D). This derived likely from a well-developed litter layer (3-5 cm) caused by dense growing *Rhc* krummholz with a high input of litter, and thus input of OM into soils. However, litter accumulation and well-developed organic layers (Oe) suggest a decelerated decomposition of OM in this area, most likely as a consequence of the year-round lowest soil temperatures in this area (see 8.2.1).

Contrary to the results of Liptzin et al. (2012), the results of this thesis do not consider krummholz (zone C in the study area) as an area of N and P accumulation. In their study, an accumulation of nutrients resulted from an interaction of krummholz vegetation with wind. In Rolwaling, topsoil N concentrations underneath krummholz (C) did not differ significantly from the subalpine forest (AB) below (Table 5). Moreover, soil N_{min} and P_{av} concentrations were significantly lower in zone C than in AB (Table 5) suggesting that other factors like hampered decomposition including N and P mineralisation are responsible for the differences found. In line with the findings of this thesis, they found the highest topsoil C concentrations underneath krummholz, however the differences in our study were not significant compared to the subalpine forest (AB) below. In Rolwaling, litter accumulation underneath dense growing *Rhc* krummholz led to relatively high topsoil C concentrations over time. In contrast to Liptzin et al. (2012), wider topsoil C:N and lower topsoil total and available N:P ratios in the alpine tundra compared to lower elevations (forest, krummholz) point to N limitation in this area. In the alpine tundra, N limitation of primary production was also found by Bowman et al. (1993) in Colorado who detected soil conditions favoring low mineralisation rates of SOM in this area. Similar to the results of this thesis, Huber et al. (2007) found decreasing soil total C, and soil total and plant-available N concentrations with elevation which they also interpreted to result from reduced rates of mineralisation with elevation due to lower temperatures. Overall, comparing soil C:N:P stoichiometric patterns with other studies in alpine treeline ecotones is impeded by the fact that they are fully underrepresented in literature. Furthermore, a comparison with results from other studies not necessarily originating from alpine treelines is challenging, since the soil stoichiometry can vary among different study sites and spatial scales, and is among others affected by variations in abiotic environmental conditions, species composition, soil types, pedogenic processes, or plant ecological strategies (Zhao et al., 2014). Also, varying determination methods of soil nutrients were used, and different fractions for C, N, and P were considered. The topsoil C:N:P ratios from this thesis (May 2013: 370:19:1; May 2014: 457:23:1) were twofold or more higher than a global scale mean of 186:13:1 (212:15:1 for forest soils; data mostly from topsoils, 0-10 cm) suggested by Cleveland and Liptzin (2007) who determined total C:N:P ratios. The remarkably higher C:N:P ratios in the study area may result from a generally hampered litter decomposition and low soil C turnover due to low temperatures, but also from the lower P_{av} compared to total P concentrations that were used as soil component relevant for stoichiometric considerations. Compared to Liptzin et al. (2012; data from 0-10 cm), who used total nutrient ratios, the results revealed lower topsoil C:N ratios underneath the subalpine forest (zones AB in this thesis), but higher topsoil C:N ratios in krummholz (C), and especially in the alpine tundra (D). Both, topsoil C:P and N:P ratios in this thesis were considerably higher (up to tenfold) which was due to distinctly higher C and N, respectively.

Summarising, the results indicate lower decomposition rates at higher elevations leading to less mineralisation of N and P, and thus lower soil N and P availability. Resulting from a stronger decline in total and available N compared to available P, the soil N:P, N_{min}:P_{av}, and N_{min}:$NaHCO_3$-P_i ratios decrease with elevation, pointing to N shortage in alpine tundra soils. It is assumed that the altitudinal changes in stand structures themselves govern nutrient cycling by the input of C, N, and P into soils by differences in litterfall.

8.2.5 Linking soil nutrient availability and C:N:P stoichiometry to foliar C:N:P stoichiometry

Likewise to topsoil N, N_{min}, P, and P_{av} concentrations, the foliar N and P concentrations declined significantly with elevation [m a.s.l.], and with altitudinal changes in stand structures, especially at the transition from krummholz (C) to the alpine tundra (D; Table 6, supplement Manuscript 3). Besides, the results revealed a significant decrease also in foliar K and Mg concentrations with elevation [m a.s.l.], for what reason a strengthened shortage in nutrients with elevation is assumed. These results contradict findings from various authors, who understood higher foliar N and P concentrations at high elevations as an adaptation to low temperature conditions that enhance metabolic activity and growth rates (e.g. Reich and Oleksyn, 2004; Han et al., 2005). Moreover, significantly decreasing foliar nutrient (N, P, K, Mg) concentrations with elevation in the majority of the investigated species in combination with significantly decreasing topsoil N, N_{min}, P, P_{av}, K, and Mg concentrations suggests that tree growth is rather source than sink limited, i.e. tree growth declines with elevation because the ability of trees to use available C is limited due to nutrient shortage and changing environmental conditions (e.g. drought stress, Manuscripts 1, 2). Since exclusively foliar C concentrations, but not non-structural carbohydrates (NSC) were determined like for example in Hoch and Körner (2003), Shi et al. (2008), and Sveinbjörnsson et al. (2010), interpretations regarding the C limitation hypothesis (Körner, 1998a) were difficult. However, the lowest topsoil C, N, and P concentrations in the alpine tundra (D) and overall consistent foliar C concentrations with elevation suggest that -apart from a strong limitation in N and P- growth conditions in the alpine tundra are affected by a C source rather than a C sink limitation. Moreover, significantly increasing foliar C:N and C:P ratios with elevation were caused by significantly decreasing foliar N and P and not by increasing C concentrations. Thus, trees may be unable to gain as much C or nutrients as they would be able to use for growth due to low nutrient availability or drought stress (Körner, 1998a, 2012; Sveinbjörnsson et al., 2010). According to that, significant relations between foliar C:N, C:P, and N:P ratios and topsoil stoichiometric ratios in *Rhc* (Fig. 10) suggest that this species likely depends on the nutrient source (stoichiometric plasticity). However, the variability in foliar C:P and N:P ratios explained was relatively small. In some of the species (e.g. *Abies*, *Acer*, *Rhas*, *Rhc*), the foliar N:P ratios -an indicator of nutrient limitation- were significantly related to topsoil N and P availability, at least at some sampling dates but with relatively low explained variances (Table 7). Equally decreasing foliar N and P with elevation led to relatively constant N:P ratios with elevation which may be caused by a co-limitation in N and P. Overall, foliar N and P concentrations were poor indicators of topsoil N and P availability as it was also found by Bowman et al. (2003) in the alpine tundra of the Colorado Rockies. They suggested that foliar nutrient concentrations might respond to variation in the ratios of supply of soil nutrients rather than variation in the supply of a single nutrient. In general, plants in low nutrient supply ecosystems like Rolwaling were often shown to respond barely to soil nutrient availability as a consequence of adaptations, which promote conservative use, loss, and uptake of nutrients (Bowman et al., 1993). This may explain the generally complex relationships between foliar stoichiometric ratios and soil nutrient availability. Especially for the deciduous tree species (e.g. *Betula*) the relations were often not significant (Table 7), and indicated foliar nutrient concentrations more independent of changing soil nutrient availability (stoichiometric homoeostasis) (cf. Sterner and Elser, 2002; Zhang et al., 2013; Sardans et al., 2015). A main issue in the statistical analyses was that not all species occurred in each altitudinal zone (A, B, C, D). Due to that, especially *Rhc*, which was numerously existent in all zones, showed the statistically most reasonable results (Table 7). In contrast, species like *Acer* and *Betula* (A and B), and *Rhas* (C and D) were less frequent, and thus less data were available for analysing soil-foliar nutrient relationships. Overall, the results cannot fully prove the ecological relevance of soil-foliar nutrient relationships in the study area.

Apart from that, foliar N:P ratios provided insights into potential nutrient limitation in Rolwaling. According to foliar N:P malnutrition thresholds, species in the study area were overall N limited (N:P < 14). Merely *Rhc* had slightly higher means in September 2014, however not in the alpine tundra (Table 4). According to Güsewell (2004), the tree and shrub species were found being co-limited by N and P in the study area (cf. Table 6, supplement in Manuscript 3). Other studies not originating from alpine treeline ecotones reported lower (e.g.

Kang et al, 2011; Wu et al., 2012), similar (e.g. Sardans et al., 2015), and higher foliar N:P ratios (e.g. Sterner and Elser, 2002; McGroddy et al., 2004; Han et al., 2005) compared to the study area. This is likely caused by species-specific variations in foliar N:P ratios limiting a direct comparison.

In summary, the results showed that tree species in the study area may interact differently with the nutrient availability in soils. Tree growth is assumed to be rather nutrient source than sink limited, most likely due to a shortage in N. Plant nutrition is most likely coupled to a recycling of litter nutrients and does not depend on subsequent supply of nutrients from the mineral soil.

9 Conclusions

This thesis reviewed the state of the art on how soil properties affect tree growth at its upper limit in a global perspective. It specifically discussed the results in relation to ecozones and the scale-dependent importance of single factors, as well as in relation to new findings from Rolwaling. Furthermore, existing gaps in the treeline literature were identified, and it was shown in which areas new research is needed, both conceptual and geographical. The extensive case study in Rolwaling indicated a strong interaction among soil properties and variations in stand structures and tree physiognomy.

The conclusions of this thesis are:

1. The approach of quantifying previous knowledge on treeline-controlling factors is the first of its kind. This thesis shows that soil properties have not received adequate attention in treeline research, and (in combination with the findings from Rolwaling) that the role of major soil nutrients and soil moisture for a potential treeline shift has been underestimated.
2. Further information, particularly with regard to soil moisture monitoring in higher spatiotemporal resolution is necessary. To determine the role of soil moisture availability for tree growth in alpine treeline ecotones, 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.
4. The result of 7.5 ± 0.6°C for growing season mean soil temperature at treeline in Rolwaling is 1.1 Kelvin higher compared to the postulated 6.4 ± 0.7°C for alpine treelines. A broadening of the ± 0.7°C error term is suggested to cover the wide range at a local scale. This thesis suggests long-term monitoring studies at near-natural treelines in different treeline environments as an efficient tool to analyse complex treeline dynamics.

5. In Rolwaling, soil moisture and stand structures interact strongly (closed forest and krummholz vs. alpine tundra). Soil moisture patterns depend on alterations in snow cover, and modify current and potential future vegetation patterns. Year-round lowest AWCs in soils of the alpine tundra are likely caused by a higher influence of solar radiation and wind compared to canopy-covered sites. Seasonal drought stress in combination with nutrient-poor soils are suggested as critical factors constraining regeneration.
6. The treeline ecotone in Rolwaling is generally limited by soil nutrients due to pedogenic processes (podzolisation) leading to leaching of organic acids and organomineral compounds from topsoils to subsoils. Nutrient availability (especially P) is generally limited by strongly acid soils.
7. The availability of soil nutrients, and foliar nutrient concentrations (N, P, K, Mg) decreases significantly with elevation not only for a single nutrient but generally, and might explain why treeline shift and global warming are decoupled.
8. Litter input and mineralisation decrease with elevation, resulting in low accumulation of SOM, and low N and P availability in alpine tundra soils. Caused by a stronger decline in total and available N than available P, the soil N:P, N_{min}:P_{av}, and N_{min}:$NaHCO_3$-P_i ratios decrease with elevation, indicating N shortage in alpine tundra soils.
9. Contrary to previous findings, the Rolwaling alpine treeline ecotone is not considered as an area of nutrient accumulation. Moreover, the altitudinal variations in stand structures themselves govern nutrient cycling by the input of C, N, and P into soils by differences in litterfall.
10. This thesis suggests that specific combinations of soil properties as well as single soil properties (low soil nutrient availability, limited soil moisture supply) may limit tree growth even below climatic treelines.

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11 Appendix

Personal Contribution

EBERHARD KARLS
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Mathematisch-
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Fakultät

Erklärung nach § 5 Abs. 2 Nr. 7 der Promotionsordnung der Math.-Nat. Fakultät
- Anteil an gemeinschaftlichen Veröffentlichungen -
Nur bei kumulativer Dissertation erforderlich!
Declaration according to § 5 Abs. 2 No. 7 of the PromO of the Faculty of Science
- Share in publications done in team work -

Name: Michael Müller

List of Publications

1. How do soil properties affect alpine treelines? General principles in a global perspective and novel findings from Rolwaling Himal, Nepal
2. Soil temperature and soil moisture patterns in a Himalayan alpine treeline ecotone
3. Soil and foliar C:N:P stoichiometry in an alpine treeline ecotone
4. Nutrient deficiency in soils and trees of a treeline ecotone in Rolwaling Himal, Nepal
5. Do Himalayan treelines respond to recent climate change? An evaluation of sensitivity indicators
6. Treeline responsiveness to climate warming: Insights from a krummholz treeline in Rolwaling Himal, Nepal

Nr	Accepted for publication yes/no	Number of all authors	Position of the candidate in list of authors	Scientific ideas of candidate (%)	Data generation by candidate (%)	Analysis and interpretation by candidate (%)	Paper writing by candidate (%)
1	yes	6	1	70	95	80	90
2	yes	5	1	70	80	90	95
3	no	5	1	70	95	90	95
4	no	6	2	50	50	50	50
5	yes	11	9	< 5	5	5	< 5
6	yes	7	3	5	15	10	5

I certify the above statement is correct.

Date, Signature of the candidate

I/We certify the above statement is correct.

Date, Signature of the doctoral committee or at least of one of the supervisors

Manuscript 1 (published)

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

Progress in Physical Geography 40(1) (2016) 135-160

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Keywords: drought stress, Himalaya, Nepal, soil nutrients, soil temperature, treeline.

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 ± 0.6°C for growing season mean soil temperature at treeline in Rolwaling is 1.2 K higher compared to the postulated 6.4 ± 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. 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 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 (Wieser and Tausz, 2007; Holtmeier, 2009; Körner, 2012). 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 Körner, 1998a, 2003a, 2012; Holtmeier, 2009) 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., Körner, 1998a, 1998b, 2007, 2012; Körner and Paulsen, 2004; Wieser and Tausz, 2007; Holtmeier, 2009). 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., Weih and Karlsson, 2001; Hoch and Körner, 2003, 2009; Smith et al., 2003; Holtmeier and Broll, 2007, 2010; Macias-Fauria and Johnson, 2013; Sullivan et al., 2015).

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., Körner, 1998a, 1998b, 2003a, 2007, 2012; Körner and Paulsen, 2004; Harsch et al., 2009; Holtmeier, 2009). 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., Loomis et al., 2006; Gehrig-Fasel et al., 2007; Treml and Banaš, 2008; Liptzin et al., 2012; McNown and Sullivan, 2013). 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 (Miehe and Miehe, 2000; Holtmeier, 2009; 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 Materials and methods

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 (Appendix S1 in supplement 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).

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

In this review, we carried out a 5-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 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).

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

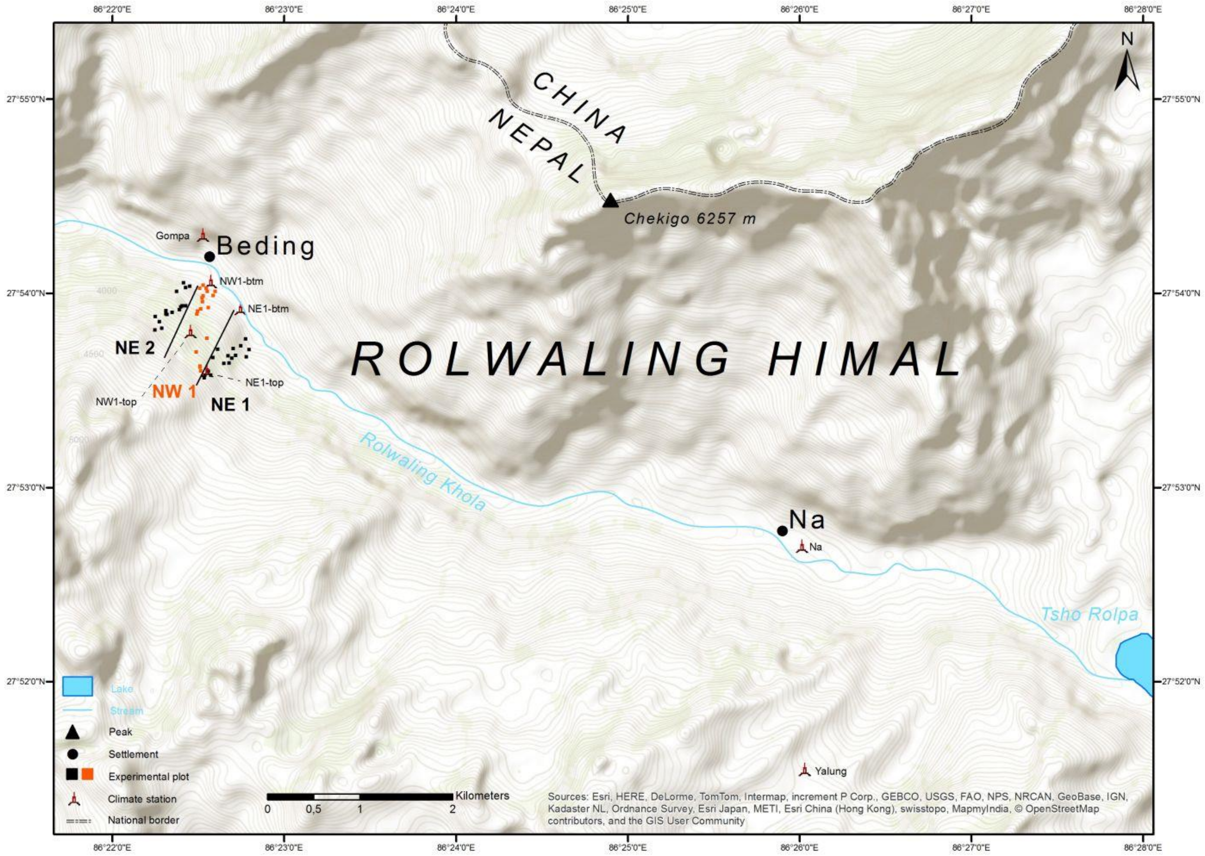
(b) $Index\ [2] = Index\ [1] \times \frac{\sum c1 + \cdots + c5}{\sum n}$

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

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 (Appendix S2, supplement 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).



Sources: Esri, HERE, DeLorme, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

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).

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, 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 (2x NE exposed slopes, 1x NW exposed slope; Fig. 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 x 20 m) were randomly selected. In total, 48 plots were sampled (3 transects x 4 altitudinal zones x 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 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 *WiFi* plant sensors (Koubachi AG) were installed along two altitudinal transects (2 transects (NE2, NW1) x 4 altitudinal zones x 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 *WiFi* 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 m^{-2} dm^{-1}).

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., Körner, 1998a, 2012; Holtmeier, 2009). 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.

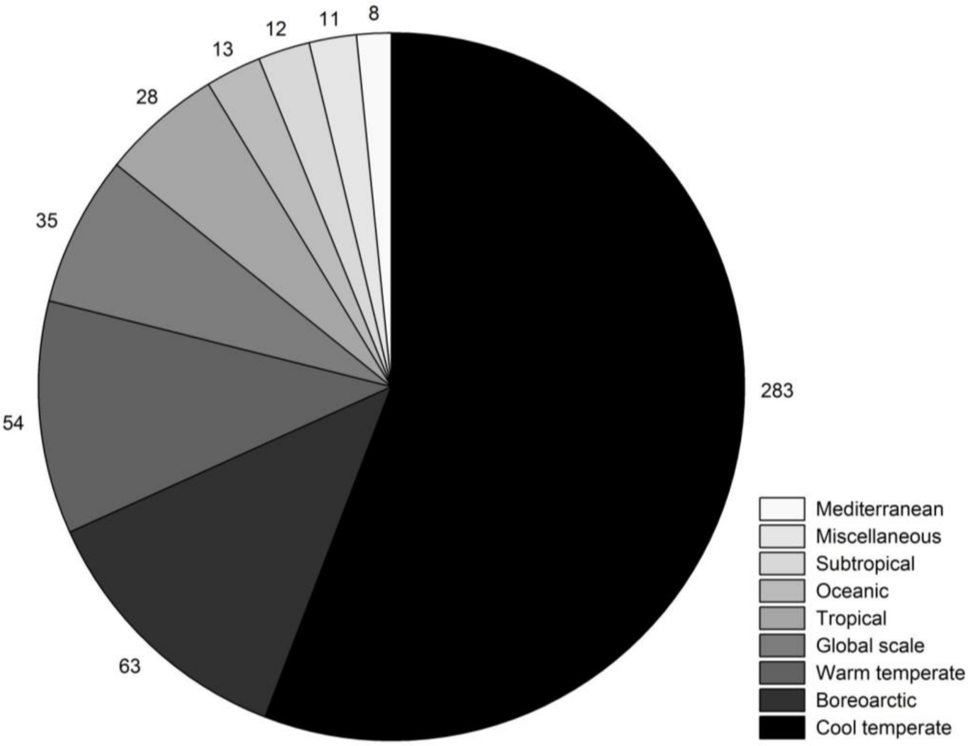


Figure 2. Reviewed treeline literature (n = 507) according to the investigated ecozone (n = 472) related to global scale studies (n = 35). Finer-scale studies are distinguished into seven different ecozones (boreoarctic, cool temperate, Mediterranean, oceanic, warm temperate, subtropical, and tropical).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

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 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 3a). The term air temperature affecting tree growth in general includes growing season mean air temperature, and minimum air temperature thresholds. In the following, we 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 3a). 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 or 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 3a). 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 3a). 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., Wang et al., 2011; Bergh et al., 2014; Kanzler et al., 2015), 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 3a), 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 funghi are highly underrepresented in treeline literature. For that reason we excluded them from Figures 3a and 3b.

Interestingly, we found major differences in the relevance of treeline-controlling factors for tree growth in different ecozones (Figure 3b). 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 3b). 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 3b). On oceanic island (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 3a) and the ecozones (Figure 3b) 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.

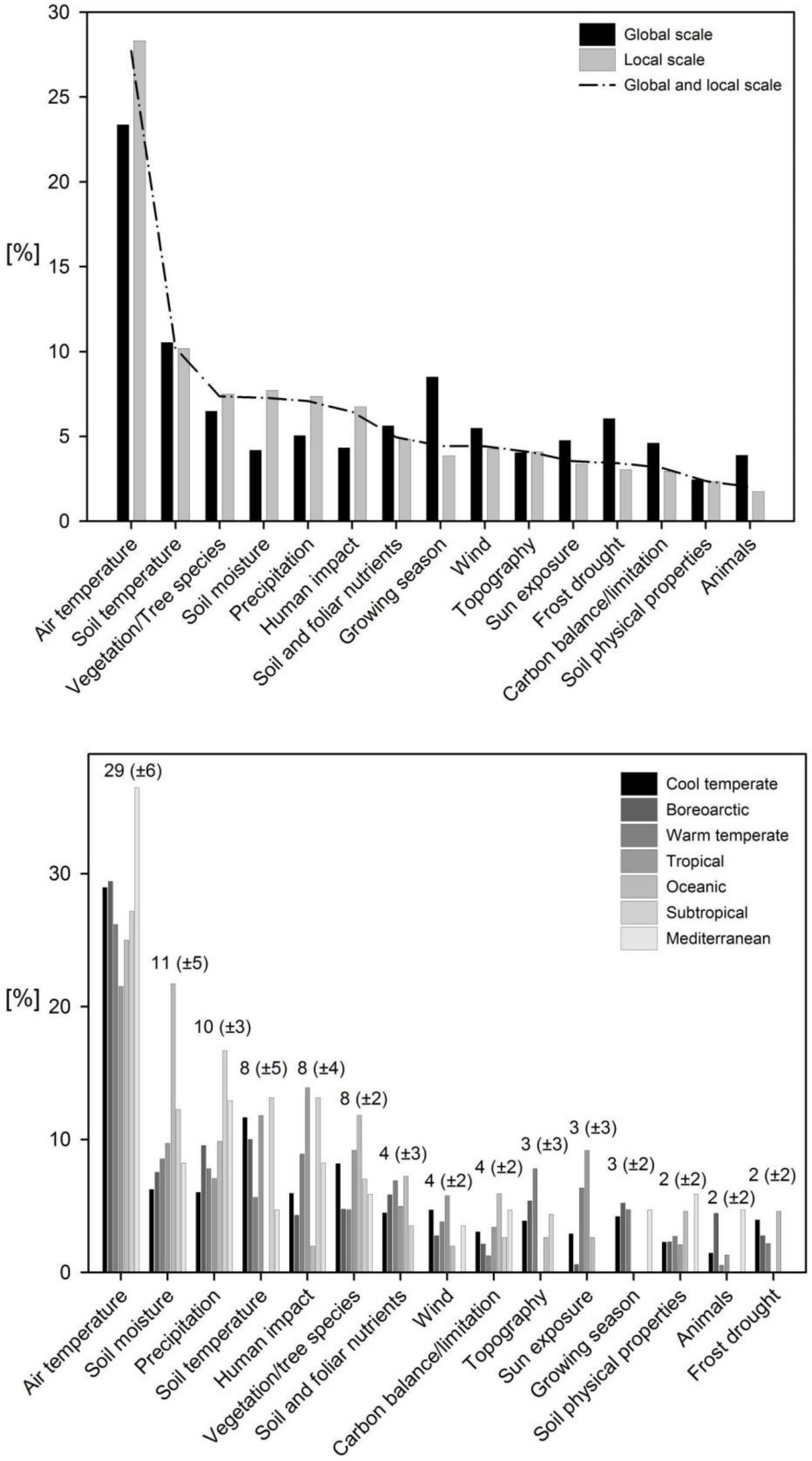


Figure 3. Relative importance (%) of factors controlling tree growth at its upper limit regarding (a) different spatial scales and (b) different ecozones. Studies including different spatial scales (miscellaneous) are excluded from Figure 3(b). Mean ± standard deviation is given for each ecozone.

Overall, our review indicates that, at a global scale, the majority of studies in current literature implicates growing season mean air and soil temperatures as the most important limiting factors for tree growth at its upper limit (Figure 3a). A similar pattern was found for the local scale (Figure 3a). 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 3a), and vary greatly between the different ecozones (Figure 3b). 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., Seastedt and Adams, 2001; Gruber et al., 2009a, b; Schmid et al., 2009; Liu and Luo, 2011; Dawes et al., 2014, 2015). Many studies focus on soil temperature (n = 88; e.g., Aulitzky, 1960; Walter and Medina, 1969; Havranek, 1972; Green, 1983; Körner, 1998a; Körner and Paulsen, 2004), whereas, related to the total amount of studies, only few authors also investigate treeline soil (n = 28) and foliar nutrient status (e.g., Shiels and Sanford, 2001; Weih and Karlsson, 2001; Köhler et al., 2006; Loomis et al., 2006; Li et al., 2008; Liptzin and Seastedt, 2009; Liptzin et al., 2012; McNown and Sullivan, 2013). 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 (Shiels and Sanford, 2001; Holtmeier and Broll, 2007; Stöhr, 2007; Holtmeier, 2009). Trees or tree stands control soil temperatures and soil moisture, root growth, nutrient uptake, mineralization and decomposition (Broll and Holtmeier, 1994; Holtmeier and Broll, 2007; Stöhr, 2007; Holtmeier, 2009). 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, supplement data). 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, 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 3a). 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 3b). Several authors (e.g., Körner, 1998a, 2012; Körner and Paulsen, 2004; Dong et al., 2011) 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., Havranek, 1972; Stöhr, 2007; Dong et al., 2011), root respiration and root water uptake (Walter and Medina, 1969; Walter, 1973; Mayr, 2007), 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 (Tranquillini, 1979; Körner, 2003b; Kullman, 2007; Stöhr, 2007; Holtmeier, 2009).

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 and Paulsen, 2004; Körner, 2012). 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 at 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 at 10 cm soil depth, however some authors report from data measured at 5 cm or deeper (15, 20, 30, 50 cm) or in differing time periods (e.g., Walter and Medina, 1969; Wininger, 1981; Bendix and Rafiqpoor, 2001; Karlsson and Weih, 2001; Hättenschwiler et al., 2002; Rossi et al., 2007; Cierjacks et al., 2008; Hertel and Wesche, 2008; Sveinbjörnsson et al., 2010; Liu and Luo, 2011; Greenwood et al., 2015), which are not included in Table 2. A growing season mean soil temperature of 5.8°C at 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). 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 treeline position, the treeline in Rolwaling would be located 500 to 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 3b), 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.

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	7.5 ± 0.5	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

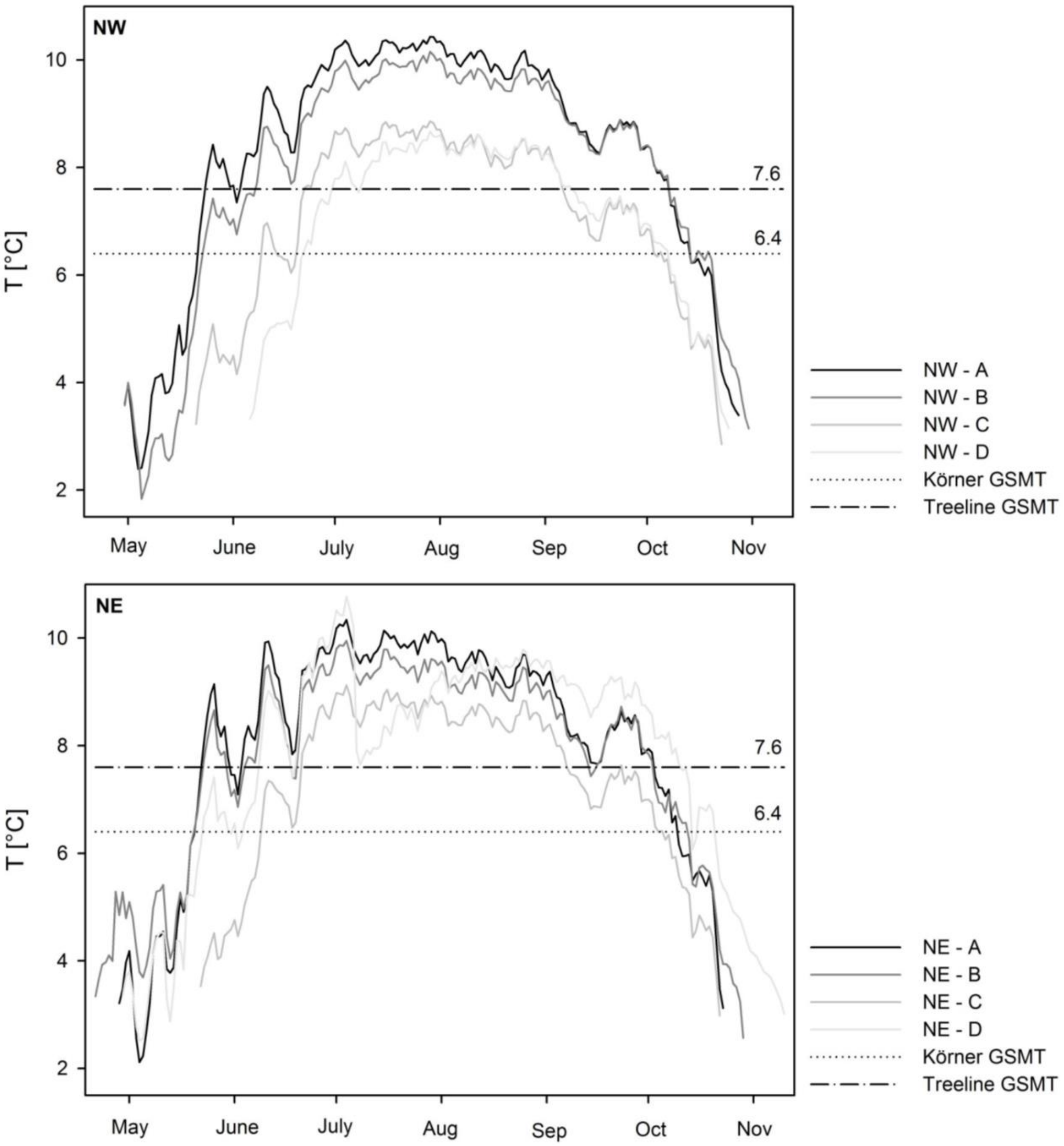


Figure 4. Daily mean soil temperatures of altitudinal zones A (closed forest), B (closed forest), C (krummholz zone) and D (dwarf shrub heath) on a NE- and a NW-exposed slope and growing season mean soil temperature (GSMT, 7.6°C, 10 cm depth) at treeline (transition zones B to C) in Rolwaling Himal, 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).

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., Kessler and Hohnwald, 1998; Bendix and Rafiqpoor 2001; Bader et al., 2007; Oberhuber, 2007; Wieser and Tausz, 2007; Gruber et al., 2009b; Holtmeier and Broll, 2010). 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; Körner 1998a, 2012; Doležal and Šrutek, 2002; Germino et al., 2002; Holtmeier, 2009). 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 3a). With regard to ecozones (Figure 3b) 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; Slatyer, 1976; Shrestha et al., 2007).

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-) 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., Peterson, 1998; Daniels and Veblen, 2004; Wilmking et al., 2006; Holtmeier and Broll, 2007; Shrestha et al., 2007; Batllori and Gutiérrez, 2008; Holtmeier, 2009; Richardson and Friedland, 2009; Barbeito et al., 2012).

Low soil water availability during different time periods of the year was found to affect tree growth and seedling establishment in all ecozones (Ferrar et al., 1988; Öberg and Kullman, 2012; Gaire et al., 2014; Liang et al., 2014), and particularly in arid and semi-arid subtropical or oceanic island treeline ecotones (cf. Figure 3b; Leuschner and Schulte, 1991; Gieger and Leuschner, 2004; Morales et al., 2004; Lara et al., 2005; Köhler et al., 2006; Fajardo et al., 2011). 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 Rolwaling, we calculated spatial and temporal variation in soil available water capacity (AWC; L m^{-2} dm^{-1}; Figure 5). Hourly year-round measurements show soil available water capacities between 6 and 10 L m^{-2} dm^{-1} 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 m^{-2} dm^{-1} 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, b, 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.

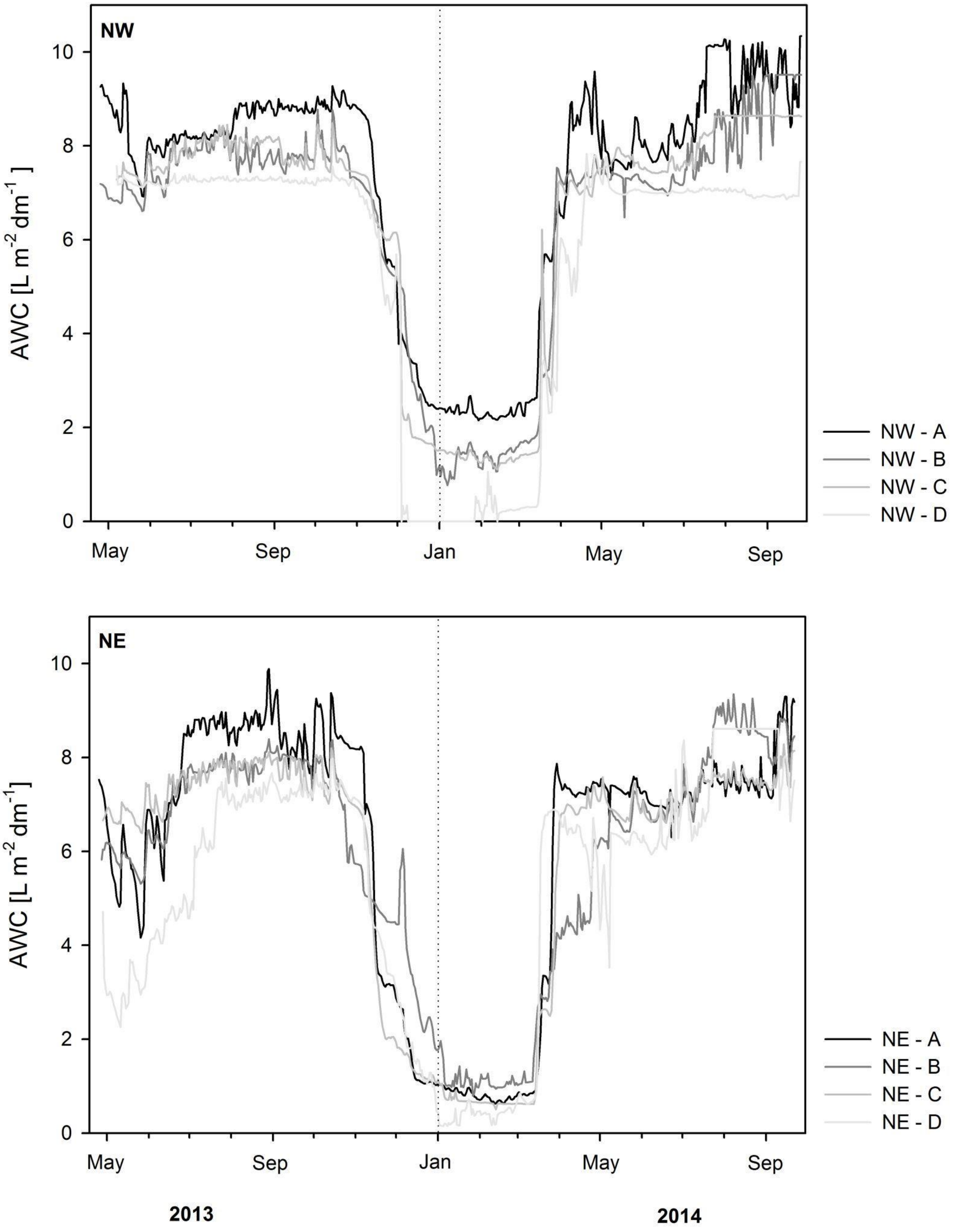


Figure 5. Spatial and temporal variation in available water capacity (AWC; L m^{-2} dm^{-1}) in altitudinal zones A (closed forest), B (closed forest), C (krummholz zone) and D (dwarf shrub heath) on a NE- and a NW-exposed slope in Rolwaling.

c Soil nutrients. A considerable number of studies (e.g., Körner, 1989; Karlsson and Nordell, 1996; Sveinbjörnsson, 2000; Birmann and Körner, 2009; Macek et al., 2012; Fajardo et al., 2012, 2013) focus on nutrient uptake and investment by plants within alpine treeline ecotones, whereas only a few concentrate on nutrient status and availability in soils (Weih and Karlsson, 2001; Köhler et al., 2006; Loomis et al., 2006; Zhang et al., 2011; Liptzin et al., 2012; McNown and Sullivan, 2013; Thébault et al., 2014; Sullivan et al., 2015). 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 3a). 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 3b). 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 (Körner, 1989, 1998b, 2003b, 2012; Weih and Karlsson, 2001; Hoch et al., 2002; Hoch and Körner, 2003; Bansal and Germino 2008; Hertel and Wesche, 2008; Shi et al., 2008; Liptzin et al., 2012; Fajardo et al., 2012, 2013). 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; Smith et al., 2003; Seastedt et al., 2004). Following this, C as a soil nutrient is thought not to be directly relevant to treeline tree growth. Trees are assumed 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 3b) assessed lower N cycling rates (e.g., nitrification and denitrification) and contents in treeline soils compared to soils at lower altitudes (Sveinbjörnsson, 2000; Frangi et al., 2005; Loomis et al., 2006; Shi et al., 2006; Huber et al., 2007; Wittich et al., 2012; McNown and Sullivan, 2013; Thébault et al., 2014; Sullivan et al., 2015), as well as lower tissue N contents in treeline trees (Garkoti and Singh, 1992, 1994; Sveinbjörnsson, 2000; Gieger and Leuschner, 2004; Richardson, 2004; Köhler et al., 2006; Shi et al., 2006; Huber et al., 2007; Wittich et al., 2012; McNown and Sullivan, 2013; Sullivan et al., 2015). 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 (Sveinbjörnsson, 2000; Loomis et al., 2006). 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 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 (Sveinbjörnsson, 2000; Loomis et al., 2006; Huber et al., 2007; McNown and Sullivan, 2013). 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 (2012) (> 3m 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 Zimmermann et al., 2010; Speed et al., 2015), 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).

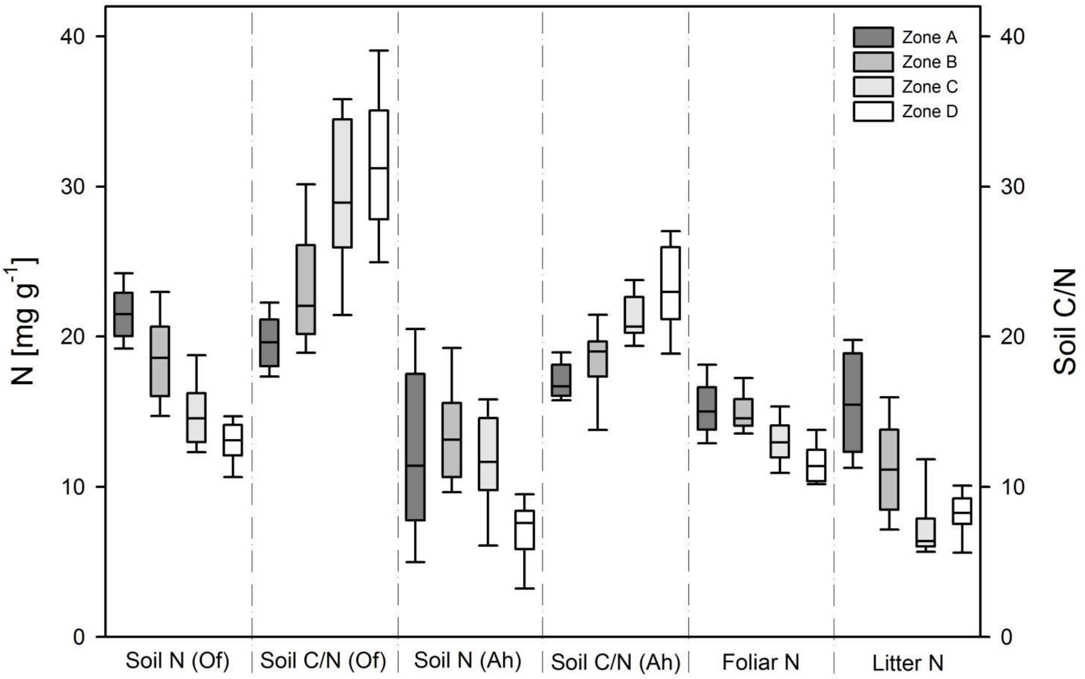


Figure 6. Nitrogen (N) concentrations [mg g^{-1}] in soils (Of layer, Ah horizons), foliage (*Rhododendron campanulatum*) and litter, and soil C/N ratio (Of, Ah) in altitudinal zones A (closed forest), B (uppermost closed forest), C (krummholz) and D (dwarf shrub heath) on NE- and NW-exposed slopes in Rolwaling Himal.

Significantly increasing 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 podzolisation 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 podzolisation 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.

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 $\alpha = 0.01$.

		Spearman correlation		**Kruskal Wallis**		**Post-hoc Nemenyi (Tukey)**					
Nutrient	**Sample material**	**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 $\alpha = 0.01$.

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 ± 0.6°C for growing season mean soil temperature at treeline in Rolwaling is 1.2 K higher compared to the postulated 6.4 ± 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 podzolisation 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.

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Supplement data

Due to excessive file sizes, the Appendices S1 and S2 (available online) were excluded from this thesis.

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Manuscript 2 (accepted)

Soil temperature and soil moisture patterns in a Himalayan alpine treeline ecotone

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Abstract

Soil properties in alpine treeline ecotones are insufficiently explored. In particular, an extensive monitoring of soil moisture conditions over a longer period of time is rare, and the effects of soil moisture variability on alpine treelines have not received adequate attention yet. Soil temperature patterns are generally well documented, and soil temperature is considered a key factor in limiting tree growth at both global and local scales.

We performed a 2 ½-year monitoring in a near-natural treeline ecotone in Rolwaling Himal, Nepal. In this paper, we present new findings on spatiotemporal soil temperature and moisture variability in relation to topographical features and vegetation patterns (variations in stand structures and tree physiognomy). Our results show a growing season mean soil temperature of 7.5 ± 0.6°C at 10 cm depth at the Rolwaling treeline. Multivariate statistical analyses yield a significant relation between soil temperatures and the variability in tree height, crown length, crown width, and LAI. In turn, soil temperature variability is controlled by the tree physiognomy itself. Soil moisture conditions (available water capacity, 0-10 cm) appear to be less substantial for current stand structures and tree physiognomy. In turn, tree physiognomy patterns control soil moisture, which additionally is affected by snow cover. In Rolwaling, shallow and coarse-grained soils cause low water-holding capacities, and thus a remarkable amount of water percolates from topsoils to subsoils. In the alpine tundra with missing forest canopy, year-round lowest available water capacities are additionally caused by high solar radiation, wind, and thus high evaporation. We assume low soil moisture availability causing largely prevented tree regeneration especially in the alpine tundra.

We conclude that soil temperature and moisture patterns reflect tree physiognomy patterns. The latter cause disparities in soil temperature and moisture conditions inside and outside of the closed forest by shading effects and differences in leaf fall.

Introduction

Tree growth at high altitudes is assumed being limited by heat deficiency (low air and soil temperatures, e.g. Körner, 1998a, 1998b, 2012; Körner and Paulsen, 2004; Wieser and Tausz, 2007; Holtmeier, 2009). A considerable number of soil temperature (ST) data is available from alpine treelines around the globe (Müller et al., 2016). At a global scale, a growing season mean ST of 6.4 ± 0.7°C has been suggested as a threshold temperature under trees at treeline elevations (Körner, 2012). At a local scale, a wide range of 5 to 12°C occurs worldwide for growing season mean ST at alpine treelines (Müller et al., 2016). Many researchers had discussed, whether tree growth in alpine treeline ecotones is limited solely by low temperatures (e.g. by an impact on meristematic processes or on photosynthesis; Hoch and Körner, 2005, 2009), or whether it is limited or modified by different abiotic and biotic factors (e.g. Holtmeier, 2009; Körner, 1998a, 2012). A detailed overview of the state of knowledge with regard to the effects of soil properties on tree growth is given in Müller et al. (2016). In contrast to ST data from the immediate vicinity of alpine treeline elevations, spatiotemporal ST data for entire treeline ecotones including subalpine forest and alpine tundra are rare and mostly cover short monitoring periods of < 1 year only (e.g. Walter and Medina, 1969; Liu and Luo, 2011; McNown and Sullivan, 2013; Paulsen and Körner, 2014).

Only a few studies investigated soil moisture (SM) and its effect on tree growth at high altitudes in more detail to date (Leuschner and Schulte, 1991; Gieger and Leuschner, 2004; Köhler et al., 2006; Liu and Luo, 2011; Öberg and Kullman, 2012; McNown and Sullivan, 2013; Paulsen and Körner, 2014; Peters et al., 2014). Thus, spatiotemporal distribution patterns of SM conditions in alpine treeline ecotones are insufficiently documented in literature (Müller et al., 2016). In general, modeling of plant-water relations is impeded due to an overall heterogeneous mountain terrain, and the hardly determinable rooting depths of plants (Paulsen and Körner, 2014). At a local scale, alpine treelines vary in SM available for plant growth, which in turn highly depends on the winter snow cover, and its removal and redeposition by wind (Hessl and Baker, 1997; Hättenschwiler and Smith, 1999; Malanson et al., 2011; Paulsen and Körner, 2014). Some case studies in different treeline environments have shown tree growth at treelines to be constrained by low SM availability rather than by low ST (Leuschner and Schulte, 1991; Liang et al., 2014; González de Andrés et al., 2015). It has been suggested that growth conditions for trees and young growth are impeded by water shortage prior to the growing season caused by an insufficient snow cover in winter, and by still frozen soils in spring, respectively (Balducci et al., 2013). During summer, increasing SM stress may also result from a warming-induced earlier onset of snowmelt (Öberg and Kullman, 2012). Further, SM stress has been demonstrated to constrain seedling establishment (e.g. Weisberg and Baker, 1995; Hessl and Baker, 1997; Lloyd and Graumlich, 1997; Camarero and Gutiérrez, 2004; Daniels and Veblen, 2004; Holtmeier and Broll, 2010; Moyes et al., 2015), and tree growth in different alpine treeline ecotones (e.g. Jacoby and D'Arrigo, 1995; Lloyd and Graumlich, 1997; Öberg and Kullman, 2012). A literature review by Müller et al. (2016) concluded that tree growth at semi-arid to arid subtropical, and oceanic island treelines is predominantly affected by seasonal drought stress (e.g. Leuschner and Schulte, 1991; Biondi, 2001; Daniels and Veblen, 2004; Gieger and Leuschner, 2004; Morales et al., 2004; Lara et al., 2005). However, the latter outcome would gain in importance if there were a larger amount of studies not only from those regions, but from a greater variety of treeline environments (Müller et al., 2016). In contrast, some studies do not attribute SM a major role in controlling tree growth, at least at a global scale (e.g. Hoch and Körner, 2005). This holds true for a treeline ecotone in the Sergyemla Mountains, Tibet, where Liu and Luo (2011) could not find a significant relationship between SM variability, and vegetation and topographical patterns. With regard to the Himalaya, information on ST and SM patterns, and their interactions with vegetation patterns is scarce. Therefore, the aims of this study were:

1. to monitor and analyze spatiotemporal ST and SM data from a near-natural treeline ecotone in Rolwaling Himal, Nepal over a longer period of time, and
2. to determine the interactions between ST and SM, topography and variations in stand structures and tree physiognomy at a local scale.

Materials and Methods

STUDY AREA

The study area is located in the northeast part of Central Nepal (N 27°54’, E 86°22’, Fig. 1). The experimental area is situated on the unsettled north-exposed slope opposite to the village of Beding in Rolwaling Himal.

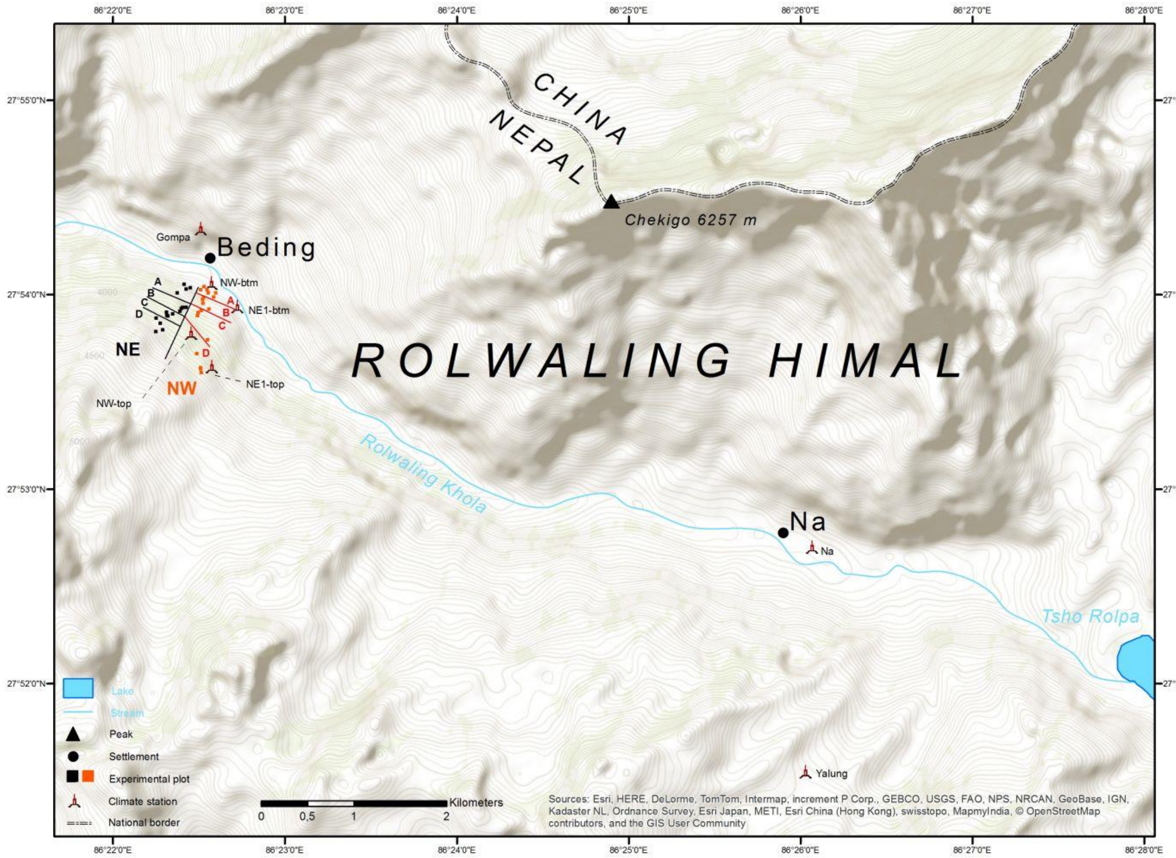

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FIGURE 1. Study area and monitoring sites for soil temperature and soil moisture in Rolwaling Himal, Nepal. Experimental design includes two investigated altitudinal transects (NE = Northeast exposition (black), NW = Northwest exposition (red)) including four altitudinal zones (A, B, C, D), and location of experimental plots and climate stations (btm = bottom, top, Gompa, Na, Yalung). The map is adopted and modified from Müller et al. (2015).

Upper subalpine forests are primarily composed of *Betula utilis* and *Abies spectabilis*, with *Rhododendron campanulatum*, *Sorbus microphylla*, *Acer caudatum*, and *Prunus rufa* forming a second tree layer (Schwab et al., 2016). Closed forests merge into a broad krummholz belt of *Rhododendron campanulatum* at ca. 3900 m a.s.l. (NW exposition, cf. Figs. 1, 2) and ca.

4000 m a.s.l. (NE exposition) respectively, which gives way to alpine tundra (*Rhododendron* dwarf scrub heaths) at ca. 4000 m a.s.l. and 4100 m a.s.l., respectively. Dwarf shrubs are interspersed by a small number of low growing individuals (diameter in breast height (dbh) < 7 cm) or young growth of *Abies spectabilis*, *Betula utilis*, and in higher amount of *Rhododendron campanulatum*. Occasionally, *Sorbus microphylla* individuals with dbh ≥ 7 cm occur (Schwab et al., 2016). Total plant species richness decreases from the closed forests in the subalpine zone across the treeline ecotone and increases again in the uppermost dwarf scrub heath at the transition to alpine grassland. Due to isolation and a very low population density of the Rolwaling valley, and virtually pristine vegetation, the treeline ecotone is considered as near-natural (Schwab et al., 2016).

Soils in the study area were classified as Podzols (according to IUSS, 2006), characterized by a substantial outwash of soil organic matter and sesquioxides from topsoil to subsoil (podsolization). Podzols showed the typical sequence of L-Of-Ah-Ae-Bh-Bs horizons. Litter cover strongly decreases from closed forest resp. krummholz to the alpine tundra.

EXPERIMENTAL DESIGN AND DATA COLLECTION

We used a stratified random sampling design with two transects (NE = Northeast exposition, NW = Northwest exposition, Figs. 1, 2) across the treeline ecotone divided into four altitudinal zones: A (closed forest), B (uppermost closed forest), C (krummholz), and D (dwarf scrub heath/alpine tundra, Figs. 1, 2). Within each zone of each altitudinal transect, four different plots (20 m x 20 m, projected on a horizontal plain) were randomly selected (Figs. 1, 2).

On 32 plots (2 transects x 4 altitudinal zones x 4 plots, Fig. 2) *Koubachi WiFi plant sensors* (Koubachi AG) monitored ST (°C) and SM (pF) every hour at 10 cm depth from April 2013 to October 2015, respectively. Additionally, two sensors were placed underneath the uppermost individuals of *Abies spectabilis* (c. 5-10 m high) and *Betula utilis* (c. 5 m) on NE transect (equivalent to the transition from zone B to C). The sensors were modified for outdoor usage to log ST from –10°C to +55°C, and pF (decadic logarithm of the absolute value of soil water tension, non-dimensional) from 0 to 5.75. We use lithium batteries, which ensure energy supply under harsh climatic conditions. Data were obtained via *WiFi* interface. For calculation of growing season mean ST, we used the well-accepted definition of growing season by Körner and Paulsen (2004), when daily mean ST at 10 cm depth first exceed 3.2°C until they drop again below 3.2°C.

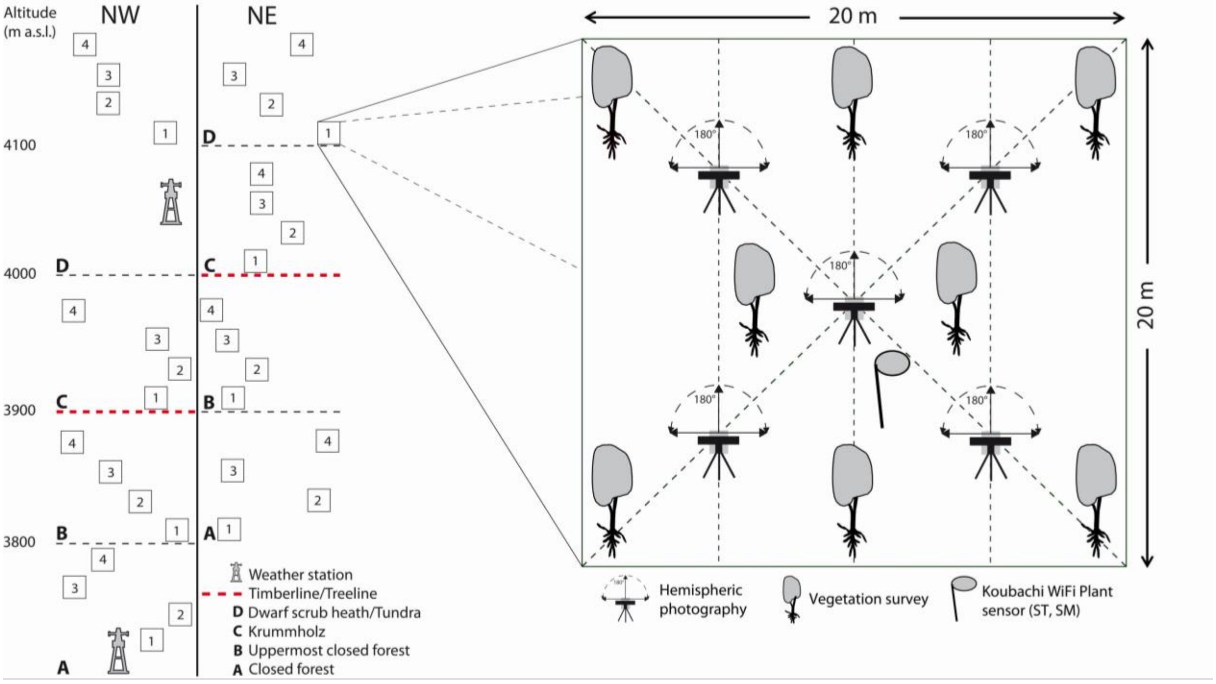

FIGURE 2. Experimental design. Schematic illustration of the two different altitudinal transects (NE = Northeast exposition, NW = Northwest exposition) including four experimental plots (20 m x 20 m) respectively in each altitudinal zone (A, B, C, D). Plot design (right) is equivalent on each plot. *Koubachi WiFi plant sensors* are available on both transects.

SM was determined as soil water content (Vol.-% resp. L m^{-2} dm^{-1}) from pF based on linear regression equations derived from default charts in Ad-hoc-Arbeitsgruppe Boden (2005) (cf. Table 3). Available water capacity (AWC, Vol.-% resp. L m^{-2} dm^{-1}) was calculated from SM, soil texture and bulk density (cf. Table 3) according to Ad-hoc-Arbeitsgruppe Boden (2005). Soil texture was analyzed according to Blume et al. (2011), using a *Sedigraph III Plus Particle Size Analyzer* (Micromeritics) in the laboratory. Bulk density was determined gravimetrically after drying of the soil at 105 °C after field sampling with 100 cm³ core cutters.

Vegetation surveys took place in April, May, July and August 2013, and in September 2014. We measured diameter at breast height (130 cm, dbh), and tree height of all trees with dbh ≥ 7 cm (cf. Schwab et al. 2016). Crown length (length of crown from trunk to terminal bud), and crown width were determined according to van Laar and Akça (2007). The number of tree individuals (dbh ≥ 7 cm) was counted on each experimental plot. Leaf area index (LAI) was measured using hemispheric photography. The camera (Nikon Coolpix 8400) includes a wide-angle fisheye lens (Nikon Fisheye Converter FC-E9), which was aligned to the free sky obtaining an angle of view of 180°. Five photos per plot (cf. Fig. 2) were taken in a cross pattern at 90 cm above ground at consistent clouded sky to enable an optimal documentation of light conditions (diffuse radiation component). Photos were taken from 22.09.2014 to 27.09.2014 on NW transect, and from 09.09.2014 to 21.09.2014 on NE transect. Using HemiView software (HEMIv9), all photos were analyzed for LAI, and mean LAI per plot computed.

STATISTICAL ANALYSES

Statistical analyses were conducted using the free programming language R, version 3.1.2 (R Development Core Team, 2014) by applying R-packages *car* (Fox and Weisberg, 2011), *PMCMR* (Pohlert, 2014), *stats* (R Development Core Team, 2014), *shape* (Soetaert, 2014), *vegan* (Oksanen, 2015), and *zoo* (Zeileis and Grothendieck, 2005).

Data gaps of ST and soil pF were small (< 15 days), and were interpolated resp. extrapolated using R-packages *zoo* and *stats*. Data were transferred to ArcMap 10.1, and georeferenced based on GPS data from field measurements during soil sampling. In ArcMap, we used IDW (Inverse Distance Weighting) as deterministic method for spatial interpolation.

We performed multivariate statistical analyses to test the relation between the independent soil variables temperature (ST) and available water capacity (AWC), and the dependent vegetation variables dbh, LAI, tree height, crown width, crown length, and number of tree individuals. Due to multicollinearity, soil moisture (SM) was excluded from analyses. The large datasets of ST and AWC contained the means from each experimental plot (NE-A1 to NE-D4, NW-A1 to NW-D4) for the entire measurement period (01.05.2013 – 31.10.2015), and for the different seasons (MAM 14, 15, JJAS 13, 14, 15, ON 13, 14, DJF 13/14, 14/15, cf. Results). For the dependent variables, we also used means from each experimental plot. In a first step prior to a *Redundancy Analysis* (RDA), we applied a *Principal Component Analysis* (PCA) for each of the two datasets ST and AWC individually. The reasons for that were to avoid multicollinearity among the many variables that represent ST and AWC, respectively, and to create the best fitting model of principal components for each of the two variables before we performed a RDA. Using the principal components in a RDA, we tested the effects of ST and AWC on vegetation variables with regard to the diverse altitudinal zones (A, B, C, D), and to different aspects (NW, NE). The results were verified by applying a *Multivariate Multiple Regression* analysis (MMR), and subsequent *MANOVA/ANOVA*.

We further tested the influence of diverse environmental variables on ST, AWC, and SM by applying multivariate linear regression analyses. Therefore, we used a larger dataset consisting of the before mentioned vegetation variables complemented by soil related variables (texture, bulk density, thickness of litter layer), and topographical variables (aspect (northness = cos (exposition)), elevation in m a.s.l). To avoid multicollinearity between independent variables, we tested them using the *vif.cca* function in R. To create the best fitting model (MMR) for the explanation of all dependent variables, and of each dependent variable individually, we conducted backward selection using the *ordistep* function from the *vegan* package in R.

Results

SOIL TEMPERATURE

Mean ST (period: 01.05.2013 – 31.10.2015) at 10 cm depth showed a significant decrease with elevation (m a.s.l.) on NW transect (Spearman $r = -0.71$, $p < 0.01$). In contrast, no significant decrease was detected on NE transect ($r = -0.04$, $p = 0.88$). Also during growing season (cf. Fig. 3), NW showed a significant decline of mean ST with elevation (m a.s.l.) (2013: $r = -0.74$, $p < 0.001$, 2014: $r = -0.82$, $p < 0.01$, 2015: $r = -0.81$, $p < 0.001$) which was not found on NE (2013: $r = 0.15$, $p = 0.55$, 2014: $r = -0.01$, $p = 0.99$, 2015: $r = 0.28$, $p = 0.25$). Despite altitudinal zones A-D are located 100 m lower in elevation on NW (cf. Figs. 1, 2), mean STs during growing season of NW A-D were slightly lower (2013: 7.7 ± 0.8°C, 2014: 7.4 ± 0.8°C, 2015: 7.4 ± 0.7°C) compared to NE (2013: 7.8 ± 0.6°C, 2014: 7.7 ± 0.6°C, 2015: 7.5 ± 0.6°C). At treeline (transition from uppermost closed forest (B) to krummholz (C) we calculated a growing season mean ST of 7.5 ± 0.6°C as mean of both transects for the growing seasons in 2013, 2014, and 2015 (cf. Fig. 3). Hereby, mean STs at treeline were slightly higher or same on NW as compared to NE (Fig. 3).

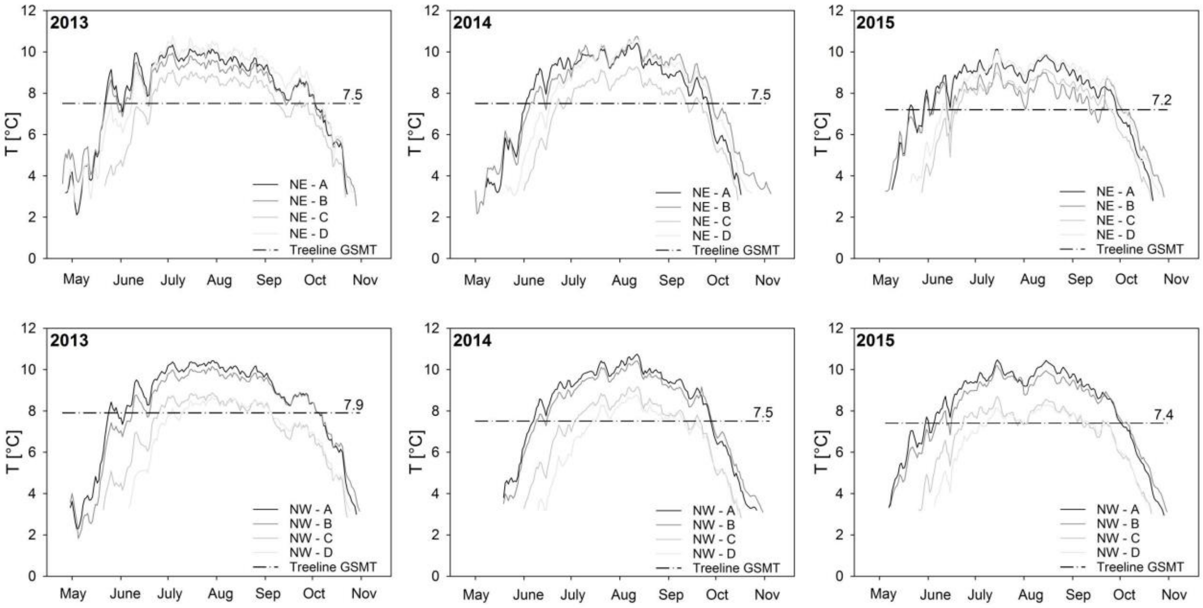

FIGURE 3. Daily mean soil temperatures during growing season in 2013, 2014 and 2015 at 10 cm depth in altitudinal zones A (closed forest), B (uppermost closed forest), C (krummholz), and D (alpine tundra) on NE (top) and NW transect (bottom). Treeline GSMT = Growing season mean temperature at 10 cm soil depth at treeline.

We found altitudinal zone-specific spatial patterns in ST. On NW, mean ST (period: 01.05.2013 – 31.10.2015) showed a strong decline from AB (4.56°C, 4.76°C) to CD (3.29°C, 2.95°C). On NE, a temperature gradient occurred from AB (4.05°C, 4.68°C) to C (3.28°C), however a higher temperature was measured in D (4.17°C). A variance analysis (Kruskal Wallis) with subsequent Post-hoc Nemenyi (Tukey) test revealed major differences ($p < 0.0001$) in daily mean ST between altitudinal zones on both transects. On NW, zones A and B ($p = 0.28$), and C and D ($p = 0.12$) showed similar variances. On NE, zones A and D ($p = 0.66$), and B and D ($p = 0.30$) did not differ significantly from each other.

With regard to different seasons, mean ST in spring (MAM) was commonly higher on NE (Table 1, Fig. 4). Contrary, we found an opposite spatial trend for autumn (ON) and winter (DJF), except for the alpine tundra (zone D). In summer (JJAS), temperature was similar on both transects, except for the alpine tundra where NE was marked by on average 2 K higher temperatures than NW (Table 1, Fig. 4).

TABLE 1 Mean seasonal soil temperatures (± s.e.) at 10 cm depth in the altitudinal zones A, B, C, and D on the NE and NW transect. AM 13 = April-May 2013, MAM = spring (March, April, May). JJAS = summer (June, July, August, September), ON = autumn (October, November), DJF = winter (December, January, February). Different letters indicate significant differences at $p < 0.05$ by Post hoc Nemenyi (Tukey) test.

Transect	Season	A	B	C	D
NE	AM 13 [1]	4.4 ± 1.2 ^{a}	5.1 ± 0.7 ^{b}	2.5 ± 1.2 ^{c}	4.7 ± 0.7 ^{d}
	JJAS 13	9.2 ± 1.2 ^{a}	8.9 ± 0.5 ^{b}	7.9 ± 0.7 ^{c}	9.4 ± 0.7 ^{a}
	ON 13	2.5 ± 1.6 ^{a}	3.3 ± 1.0 ^{ab}	2.3 ± 0.4 ^{bc}	2.9 ± 1.6 ^{c}
	DJF 13/14	-2.9 ± 2.0 ^{a}	-0.6 ± 0.7 ^{b}	-3.2 ± 1.5 ^{a}	-2.6 ± 2.0 ^{c}
	MAM 14	1.2 ± 1.5 ^{ab}	1.9 ± 0.8 ^{b}	0.2 ± 0.8 ^{a}	1.0 ± 1.0 ^{b}
	JJAS 14	9.1 ± 1.2 ^{a}	9.2 ± 1.2 ^{a}	7.6 ± 0.8 ^{b}	8.9 ± 0.6 ^{a}
	ON 14	2.0 ± 1.6 ^{a}	3.5 ± 0.8 ^{b}	1.9 ± 0.4 ^{b}	2.8 ± 1.5 ^{c}
	DJF 14/15	-1.7 ± 2.5 ^{a}	0.0 ± 0.4 ^{b}	-1.1 ± 1.2 ^{c}	-0.8 ± 1.9 ^{c}
	MAM 15	1.5 ± 1.9 ^{ac}	2.3 ± 0.8 ^{bd}	0.5 ± 0.7 ^{acd}	0.9 ± 1.1 ^{bcd}
	JJAS 15	8.8 ± 1.5 ^{a}	8.0 ± 0.6 ^{b}	7.8 ± 0.7 ^{b}	8.7 ± 0.4 ^{a}
NW	AM 13 [1]	4.2 ± 1.0 ^{a}	3.7 ± 1.2 ^{b}	2.8 ± 1.1 ^{c}	1.3 ± 0.7 ^{d}
	JJAS 13	9.5 ± 0.6 ^{a}	9.2 ± 0.7 ^{b}	7.7 ± 1.0 ^{c}	7.3 ± 0.9 ^{c}
	ON 13	3.2 ± 1.1 ^{ab}	3.9 ± 0.3 ^{bc}	2.4 ± 1.2 ^{c}	2.7 ± 0.6 ^{c}
	DJF 13/14	-1.9± 1.8 ^{a}	-0.8 ± 0.9 ^{b}	-2.4 ± 1.8 ^{a}	-2.1 ± 1.1 ^{a}
	MAM 14	0.8 ± 1.0 ^{a}	1.3 ± 0.8 ^{b}	0.0 ± 1.1 ^{a}	0.0 ± 0.6 ^{a}
	JJAS 14	9.3 ± 0.6 ^{a}	9.0 ± 0.8 ^{a}	7.4 ± 1.1 ^{b}	6.7 ± 0.6 ^{c}
	ON 14	3.0 ± 1.3 ^{a}	3.7 ± 1.0 ^{b}	2.0 ± 1.2 ^{b}	1.6 ± 0.6 ^{b}
	DJF 14/15	-0.2 ± 1.5 ^{a}	0.6 ± 1.2 ^{b}	-0.6 ± 1.6 ^{a}	-1.1 ± 0.7 ^{c}
	MAM 15	2.1 ± 0.9 ^{a}	2.2 ± 0.8 ^{a}	0.4 ± 1.1 ^{b}	-0.2 ± 0.7 ^{b}
	JJAS 15	9.3 ± 0.5 ^{a}	8.9 ± 0.5 ^{a}	7.4 ± 1.0 ^{b}	7.0 ± 0.4 ^{b}

[1] Data in April are available from 18.04.2013

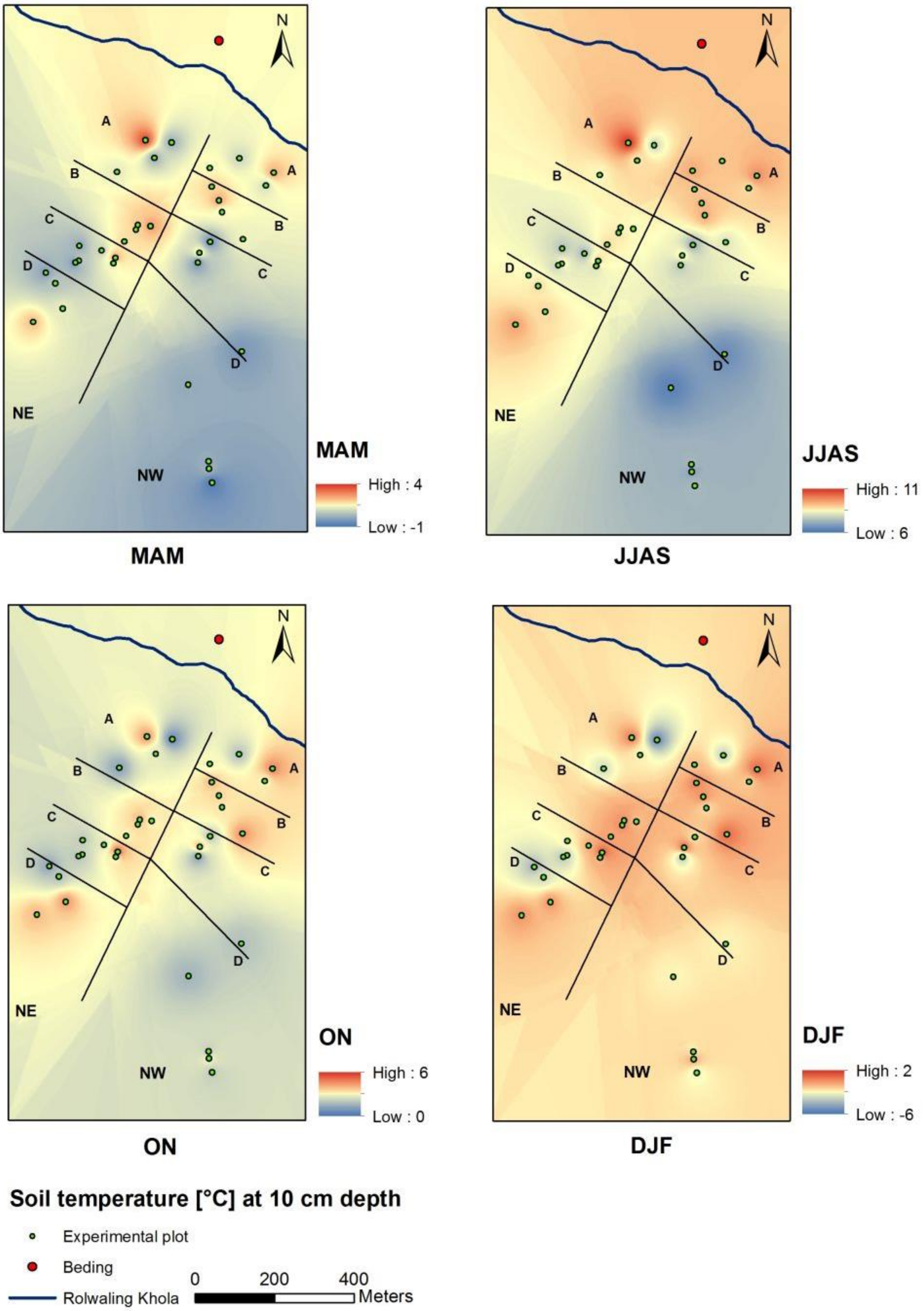

FIGURE 4. Spatiotemporal distribution of soil temperatures at 10 cm depth. A, B, C, D = Altitudinal zones. NW = Northwest. NE = Northeast. MAM = spring (March, April, May), JJAS = summer (June, July, August, September), ON = autumn (October, November), DJF = winter (December, January, February).

Overall, we measured year-round higher STs in D compared to C, and slightly higher or similar STs compared to A on NE. This was not found for NW, where lowest STs occurred in D, especially in summer (JJAS). Higher STs in D compared to C were found in ON 13 and DJF 13/14 only, and similar STs were measured in MAM 14 (Table 1). Winter (DJF) STs on both transects were similar or even colder in A compared to C and D, and were warmest in B (Table 1, cf. Fig. 4). Also in autumn (ON) and spring (MAM), higher STs were measured in B compared to A. In general, STs in winter 2014/2015 (DJF 14/15) were markedly higher than in winter 2013/2014 (DJF 13/14) (Table 1). Likewise, STs in spring 2015 (MAM 15) exceeded those of spring 2014 (MAM 14) (Table 1).

SOIL MOISTURE

Lowest mean pF values (corresponding to highest soil water tension) of 0-2 were measured in summer (JJAS) and autumn (ON), highest (corresponding to lowest soil water tension) of 2-5 were detected in winter (DJF), followed by spring months (AM 13, MAM) (Table 2). Overall, NE was pF 0.4 drier than NW. On both transect, soils in the alpine tundra revealed year-round drier pF compared to lower altitudes (Table 2). Corresponding to ST measurements showing higher values in DJF 14/15 and MAM 15 compared to the previous year (DJF 13/14, MAM 14), we found distinctly lower pF values (corresponding to higher soil water tensions) in DJF 14/15 and MAM 15 (Table 2) on both transects.

A Kruskal Wallis test with Post-hoc Nemenyi (Tukey) test of daily mean pF values (period: 01.05.2013 – 30.09.2015) on both altitudinal transects resulted in significant differences between zones ABC and D ($p < 0.0001$) (cf. Table 2). On NW, AB (0.38) did not vary significantly. On NE, AB (0.82) and AD (0.34) were similar, whereas AC, BC, BD, and CD ($p < 0.0001$) differed significantly from each other. The same tests for SM and AWC ended up in similar results. With regard to different seasons, we found a more complex spatial pattern of pF on NE than on NW (see results from Post-hoc Nemenyi (Tukey) test in Table 2). However, zone D (alpine tundra) on both transects differed from the other zones nearly in every season.

TABLE 2 Mean (± s.e.) seasonal soil pF at 10 cm depth, and soil water content (SM) and available water capacity (AWC) in Vol.-% resp. L m^{-2} dm^{-1} in the altitudinal zones A, B, C, and D on the NE and NW transect. AM 13 = April-May 2013, JJAS = summer (June, July, August, September), ON = autumn (October, November), DJF = winter (December, January, February), MAM = spring (March, April, May). Different letters indicate significant differences at $p < 0.05$ by Post hoc Nemenyi (Tukey) test.

		Soil pF				SM [Vol.-% resp. L $m^{-2}dm^{-1}$]				AWC [Vol.-% resp. L $m^{-2}dm^{-1}$]			
Transect	Season	A	B	C	D	A	B	C	D	A	B	C	D
NE	AM 13 [1]	1.9 ± 0.9 ^{a}	1.9 ± 0.7 ^{b}	1.2 ± 0.1 ^{c}	2.2 ± 0.5 ^{d}	29.0 ± 4.0 ^{a}	27.3 ± 5.4 ^{b}	30.8 ± 1.5 ^{c}	17.1 ± 7.9 ^{d}	6.8 ± 1.3 ^{a}	6.0 ± 1.2 ^{b}	6.8 ± 0.6 ^{c}	3.6 ± 2.7 ^{d}
	JJAS 13	0.9 ± 0.8 ^{ac}	1.0 ± 0.7 ^{bc}	0.7 ± 0.5 ^{abc}	1.0 ± 0.4 ^{d}	35.6 ± 5.9 ^{ac}	34.5 ± 5.5 ^{bc}	35.3 ± 4.6 ^{abc}	29.9 ± 7.1 ^{d}	8.4 ± 1.8 ^{ac}	7.6 ± 1.2 ^{bc}	7.6 ± 1.1 ^{abc}	6.3 ± 1.6 ^{d}
	ON 13	1.7 ± 0.9 ^{a}	1.9 ± 1.6 ^{b}	1.6 ± 0.3 ^{c}	1.8 ± 0.9 ^{d}	28.6 ± 1.7 ^{a}	27.7 ± 5.6 ^{b}	28.9 ± 2.1 ^{c}	27.2± 8.8 ^{d}	6.7 ± 0.8 ^{a}	6.1 ± 2.5 ^{b}	5.8 ± 0.7 ^{c}	5.7 ± 1.8 ^{d}
	DJF 13/14	4.7 ± 0.7 ^{a}	4.2 ± 0.9 ^{b}	4.5 ± 0.6 ^{b}	4.7 ± 0.7 ^{a}	3.7 ± 4.4 ^{a}	7.8 ± 5.8 ^{b}	6.9 ± 4.8 ^{b}	3.4 ± 3.2 ^{a}	0.9 ± 1.1 ^{a}	1.7 ± 1.3 ^{a}	0.9 ± 1.1 ^{b}	0.7 ± 2.5 ^{b}
	MAM 14	2.6 ± 1.1 ^{a}	2.8 ± 1.1 ^{b}	2.0 ± 0.5 ^{b}	2.8 ± 0.9 ^{c}	19.5 ± 7.2 ^{a}	19.3 ± 5.5 ^{b}	25.4 ± 2.6 ^{b}	18.7 ± 8.7 ^{c}	4.5 ± 2.8 ^{a}	4.2 ± 1.2 ^{b}	5.2 ± 0.7 ^{b}	4.0 ± 2.0 ^{c}
	JJAS 14	1.3 ± 0.4 ^{a}	1.0 ± 0.7 ^{a}	0.9 ± 0.4 ^{a}	1.4 ± 0.4 ^{b}	31.4 ± 1.2 ^{a}	34.8 ± 5.5 ^{a}	34.8 ± 4.2 ^{a}	30.1 ± 2.3 ^{b}	7.4 ± 0.7 ^{a}	7.6 ± 1.2 ^{a}	7.4 ± 1.2 ^{a}	6.3 ± 0.6 ^{b}
	ON 14	1.3 ± 0.8 ^{a}	1.8 ± 0.3 ^{b}	1.2 ± 0.4 ^{c}	1.4 ± 0.8 ^{d}	32.4 ± 4.1 ^{a}	29.4 ± 2.3 ^{b}	30.8 ± 3.1 ^{c}	28.1 ± 7.3 ^{d}	7.7 ± 1.5 ^{a}	6.0 ± 0.5 ^{b}	6.6 ± 0.9 ^{c}	6.3 ± 1.9 ^{d}
	DJF 14/15	4.1 ± 0.9 ^{a}	3.5 ± 1.2 ^{b}	3.9 ± 0.5 ^{b}	4.1 ± 0.6 ^{a}	7.7 ± 7.0 ^{a}	14.2 ± 9.2 ^{b}	13.1 ± 3.4 ^{b}	7.1 ± 9.2 ^{a}	1.8 ± 1.8 ^{a}	3.1 ± 2.0 ^{b}	1.6 ± 0.8 ^{b}	1.2 ± 1.8 ^{a}
	MAM 15	2.5 ± 1.4 ^{a}	2.4 ± 1.2 ^{b}	1.7 ± 0.4 ^{b}	2.3 ± 0.6 ^{c}	24.2 ± 3.8 ^{a}	24.3 ± 7.3 ^{b}	28.0 ± 1.9 ^{b}	23.7 ± 5.0 ^{c}	5.7 ± 0.9 ^{a}	5.3 ± 1.6 ^{b}	5.7 ± 0.4 ^{b}	5.0 ± 1.0 ^{c}
	JJAS 15	1.4 ± 0.8 ^{a}	1.7 ± 0.6 ^{b}	0.9 ± 0.4 ^{a}	1.8 ± 0.8 ^{c}	29.5 ± 3.3 ^{a}	29.4 ± 3.6 ^{b}	30.2 ± 3.5 ^{a}	27.0 ± 2.7 ^{c}	6.9 ± 0.7 ^{a}	6.5 ± 0.8 ^{b}	7.3 ± 1.0 ^{a}	5.7 ± 0.6 ^{c}
NW	AM 13[1]	1.1 ± 0.2 ^{a}	1.3 ± 0.2 ^{b}	1.2 ± 0.1 ^{c}	1.5 ± 0.1 ^{d}	32.9 ± 3.5 ^{a}	32.3 ± 1.7 ^{b}	32.3 ± 1.1 ^{c}	30.2 ± 1.7 ^{d}	7.8± 1.3 ^{a}	7.1 ± 0.4 ^{b}	7.0 ± 0.9 ^{c}	6.6 ± 1.0 ^{d}
	JJAS 13	0.9 ± 0.4 ^{ab}	0.9 ± 0.4 ^{bc}	0.9 ± 0.4 ^{bc}	1.4 ± 0.2 ^{d}	35.9 ± 3.6 ^{ab}	35.3 ± 3.4 ^{bc}	35.1 ± 3.5 ^{bc}	31.1 ± 1.8 ^{d}	8.5 ± 1. 4 ^{ab}	7.8 ± 0.7 ^{bc}	7.7 ± 1.3 ^{bc}	6.8 ± 1.0 ^{d}
	ON 13	1.1 ± 0.7 ^{a}	1.3 ± 0.5 ^{b}	1.5 ± 0.6 ^{c}	1.8 ± 0.4 ^{d}	34.0 ± 5.0 ^{a}	32.3 ± 0.8 ^{b}	29.8 ± 4.6 ^{c}	26.7 ± 1.8 ^{d}	8.0 ± 1.6 ^{a}	7.1 ± 0.2 ^{b}	6.5 ± 1.2 ^{c}	5.8 ± 0.4 ^{d}
	DJF 13/14	3.9 ± 1.3 ^{a}	4.0 ± 0.5 ^{b}	4.4 ± 0.7 ^{c}	4.9 ± 0.8 ^{d}	11.1 ± 7.8 ^{a}	8.4 ± 2.8 ^{b}	4.4 ± 4.6 ^{c}	1.6 ± 3.0 ^{d}	2.6 ± 1.9 ^{a}	1.9 ± 0.6 ^{b}	1.0 ± 1.0 ^{c}	0.3 ± 0.6 ^{d}
	MAM 14	1.7 ± 0.9 ^{a}	1.9 ± 0.2 ^{b}	2.1 ± 0.4 ^{c}	2.2 ± 0.7 ^{d}	28.6 ± 5.1 ^{a}	27.2 ± 0.9 ^{b}	24.2 ± 3.1 ^{c}	23.0 ± 3.7 ^{d}	6.8 ± 1.6 ^{a}	6.0 ± 0.2 ^{b}	5.3 ± 1.1 ^{c}	4.9 ± 0.4 ^{d}
	JJAS 14	0.7 ± 0.5 ^{a}	1.0 ± 0.2 ^{b}	0.7 ± 0.5 ^{b}	1.0 ± 0.4 ^{c}	38.0 ± 4.3 ^{a}	34.0 ± 2.5 ^{b}	36.7 ± 4.5 ^{b}	33.2 ± 2.3 ^{c}	9.0 ± 1.6 ^{a}	7.5 ± 0.6 ^{b}	8.0 ± 1.8 ^{b}	7.2 ± 1.0 ^{c}
	ON 14	1.0 ± 0.6 ^{a}	0.5 ± 0.7 ^{b}	1.1 ± 0.5 ^{c}	1.6 ± 0.4 ^{d}	35.5 ± 2.3 ^{a}	39.5 ± 4.6 ^{b}	33.2 ± 3.8 ^{c}	28.7 ± 1.4 ^{d}	8.3 ± 0.9 ^{a}	8.7 ± 1.0 ^{b}	7.3 ± 1.5 ^{c}	6.2 ± 0.9 ^{d}
	DJF 14/15	2.7 ± 1.1 ^{a}	1.6 ± 1.8 ^{a}	3.1 ± 1.1 ^{b}	3.1 ± 0.6 ^{c}	19.1 ± 9.5 ^{a}	29.0 ± 9.3 ^{a}	14.6 ± 7.1 ^{b}	13.6 ± 5.6 ^{c}	4.4 ± 2.0 ^{a}	6.4 ± 2.2 ^{a}	3.1 ± 2.1 ^{b}	3.0 ± 1.2 ^{c}
	MAM 15	1.3 ± 0.6 ^{a}	1.2 ± 0.8 ^{b}	1.8 ± 0.3 ^{c}	1.8 ± 0.3 ^{d}	32.1 ± 2.6 ^{a}	29.8 ± 7.3 ^{b}	27.1 ± 0.8 ^{c}	26.9 ± 1.1 ^{d}	7.6 ± 0.8 ^{a}	6.6 ± 1.6 ^{b}	5.9 ± 0.7 ^{c}	5.8 ± 0.7 ^{d}
	JJAS 15	0.9 ± 0.5 ^{a}	1.2 ± 0.7 ^{b}	1.2 ± 0.6 ^{c}	1.7 ± 0.3 ^{d}	36.2 ± 3.9 ^{a}	28.9 ± 7.4 ^{b}	33.0 ± 6.2 ^{c}	27.4 ± 3.0 ^{d}	8.6 ± 1.5 ^{a}	6.4 ± 1.6 ^{b}	7.3 ± 2.2 ^{c}	6.0 ± 1.0 ^{d}

[1] Data in April are available from 18.04.2013

Derived from pF values and soil texture (cf. Table 3), we calculated seasonal mean soil water content (SM, in Vol.-% resp. L $m^{-2}dm^{-1}$, 0-10 cm soil depth, Table 2). According to IUSS (2006), soil texture at 10 cm depth is sand or loamy sand. Further, available water capacity (AWC, Vol.-% resp. L $m^{-2}dm^{-1}$, 0-10 cm soil depth, Table 2, Fig. 5) was calculated from SM, texture, and bulk density (cf. Table 3). Likewise to pF, highest SM and AWC, respectively, were calculated for summer (JJAS), followed by autumn (ON), spring (MAM), and winter (DJF) (cf. Fig. 5). Both transects had year-round lowest SM and AWC in the alpine tundra (D) (Table 2). For the period from 01.05.2013 to 30.09.2015, we calculated a decline of mean AWC from A to D on both transects (NE: A = 5.53, B = 5.39, C = 5.51, D = 5.20, NW: A = 7.13, B = 6.69, C = 5.92, D = 5.40).

STAND STRUCTURE AND TREE PHYSIOGNOMY

For multivariate statistical analyses, we used tree physiognomy data from each experimental plot, which has been described previously in detail in Schwab et al. (2016). Thus, merely a brief summary of the data is presented as means of altitudinal zones (± standard error) in Table 3. Tree height, crown width, crown length, and dbh decreased with elevation. Crown width, crown length, and dbh, respectively were higher in the uppermost closed forest (B) than in the closed forest (A) on NW. On NE, the uppermost closed forest (B) showed the highest number of tree individuals (dbh ≥ 7 cm), whereas on NW most individuals occurred in krummholz (C). LAI was similar in A and B, and decreased at the transition from B to C, more notable on NE. LAI declined sharply in the alpine tundra (D) on both transects. In general, all investigated vegetation variables indicate higher values on NE.

In Table 3, we also included results from soil texture and soil bulk density. Soil texture is commonly very homogeneous throughout the study area with generally coarse grain sizes (proportion of sand > 60 %). Bulk density is overall low across the alpine treeline ecotone (~ 1 g cm^{-3}) with marginal differences between altitudinal zones (Table 3).

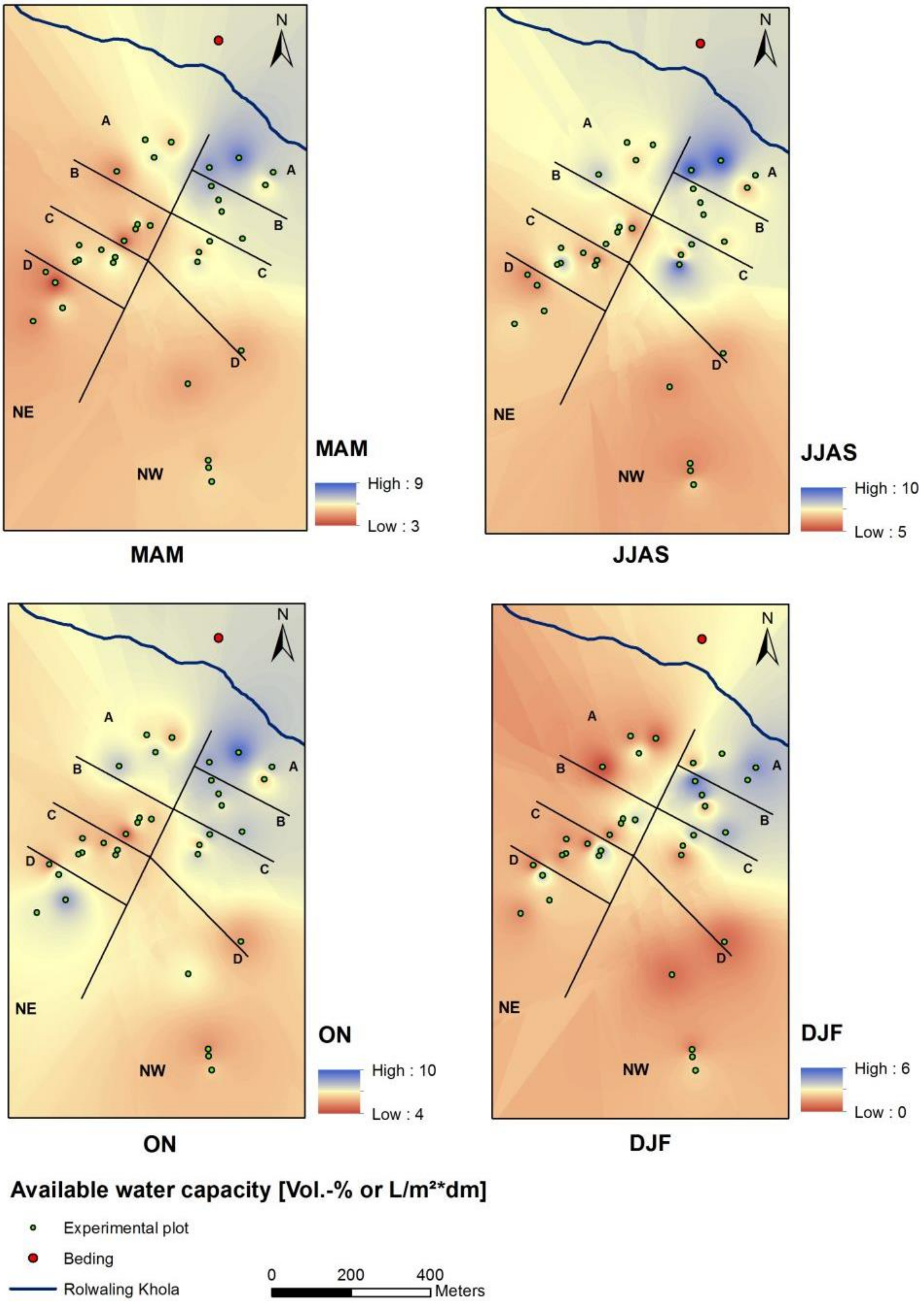

FIGURE 5. Spatiotemporal variation in available water capacity (Vol.-% resp. L $m^{-2}dm^{-1}$). A, B, C, D = Altitudinal zones. NW = Northwest. NE = Northeast. MAM = March-May, JJAS = June-September, ON = October-November, DJF = December-February.

TABLE 3 Summary of vegetation, soil texture, and bulk density data (means of altitudinal zones ± s.e.). Soil texture and bulk density were used for calculation of SM and AWC at 0-10 cm soil depth. dbh = diameter at breast height. NE = Northeast, NW = Northwest. A, B, C, D = Altitudinal zones. Different letters indicate significant differences at $p < 0.05$ by Post hoc Nemenyi (Tukey) test.

Transect - Altitudinal zone	Tree height	Crown width	Crown length	dbh	Individuals (dbh ≥ 7 cm)	Leaf area index	Sand	Silt	Clay	Bulk density
	[m]	[m]	[m]	[cm]	[n]	[LAI]	[%]	[%]	[%]	[g cm^{-3}]
NE – A	7.84 ± 1.13 ^{a}	4.24 ± 0.33 ^{a}	4.08 ± 0.74 ^{a}	16.59 ± 2.13 ^{a}	50 ± 18 ^{a}	1.74 ± 0.17 ^{a}	65 ± 2 ^{a}	27 ± 1 ^{a}	8 ± 2 ^{a}	1.24 ± 0.17 ^{a}
NE – B	5.66 ± 0.52 ^{a}	3.61 ± 0.36 ^{a}	3.08 ± 0.28 ^{a}	14.02 ± 0.72 ^{a}	96 ± 23 ^{b}	1.88 ± 0.22 ^{a}	63 ± 4 ^{a}	28± 2 ^{a}	9 ± 1 ^{a}	1.14 ± 0.09 ^{ab}
NE – C	1.94 ± 0.86 ^{b}	2.35 ± 0.13 ^{b}	0.82 ± 0.22 ^{b}	7.90 ± 0.44 ^{b}	40 ± 36 ^{a}	1.47 ± 0.14 ^{a}	68 ± 5 ^{a}	24 ± 4 ^{a}	8 ± 1 ^{a}	1.10 ± 0.11 ^{a}
NE – D	0.55 ± 1.10 ^{c}	0.38 ± 0.75 ^{c}	0.31 ± 0.63 ^{c}	1.83 ± 3.65 ^{c}	1 ± 1 ^{c}	0.14 ± 0.07 ^{b}	73 ± 6 ^{a}	19 ± 5 ^{a}	8 ± 3 ^{a}	0.97 ± 0.01 ^{b}
NW - A	5.64 ± 0.34 ^{a}	3.58 ± 0.53 ^{a}	3.24 ± 0.20 ^{a}	11.62 ± 1.86 ^{a}	42 ± 19 ^{a}	1.49 ± 0.16 ^{a}	65 ± 1 ^{a}	27 ± 1 ^{a}	8 ± 1 ^{a}	1.20 ± 0.17 ^{a}
NW - B	5.46 ± 0.74 ^{a}	4.03 ± 1.06 ^{a}	3.35 ± 0.85 ^{a}	13.90 ± 2.04 ^{a}	45 ± 13 ^{a}	1.35 ± 0.13 ^{a}	61 ± 1 ^{a}	30 ± 2 ^{a}	9 ± 1 ^{a}	1.38 ± 0.08 ^{a}
NW - C	2.47 ± 0.38 ^{b}	2.26 ± 0.15 ^{b}	1.10 ± 0.36 ^{b}	8.63 ± 0.68 ^{b}	105 ± 60 ^{b}	1.27 ± 0.27 ^{a}	69 ± 7 ^{a}	24 ± 6 ^{a}	7 ± 2 ^{a}	1.20 ± 0.14 ^{a}
NW - D	0.53 ± 1.05 ^{c}	0.28 ± 0.56 ^{c}	0.25 ± 0.50 ^{c}	1.78 ± 3.55 ^{c}	1 ± 2 ^{c}	0.11 ± 0.02 ^{b}	69 ± 7 ^{a}	23 ± 5 ^{a}	8 ± 2 ^{a}	1.07 ± 0.11 ^{a}

MULTIVARIATE STATISTICS

In a first step, a PCA including the different ST variables resulted in 70 % proportion of variance for principal component 1 (PC1) which was represented predominantly by the STs measured in the entire period (01.05.2013 – 31.10.2015), and in spring 2014 (MAM 14) and 2015 (MAM 15), respectively. 19 % proportion of variance was explained by principal component 2 (PC2) which included primarily spring temperatures in 2013 (AM 13), and winter temperatures (DJF 13/14, 14/15).

The same method applied to AWC revealed 50 % proportion of variance for PC1 (entire period, summer (JJAS)), and 31 % for PC2, mainly covered by winter (DJF), and spring (AM 13, MAM). A PCA of SM led to 40 % proportion of variance by PC1 including the entire period, spring, and summer. PC2 (34 %) was composed primarily of winter SM (DJF).

We integrated the different PCs (summarized as ST and AWC) as vector variables into a *Redundancy Analysis* (RDA) to test their relations to the dependent variables (cf. Table 3). Figure 6 indicates that ST is the most important independent variable on the first axis (RDA1), and that AWC is most important on the second axis (RDA2). The proportion explained by the RDA 1 axis was 99 %, while the RDA 2 axis represented 1 %. ST was strongly correlated with crown length and tree height. LAI, crown width, dbh, and the number of tree individuals correlated less strongly with both ST and AWC (Fig. 6).

The circles (Fig. 6a) indicate diverse groups representing differences among the altitudinal zones. Zones A and B (closed forest, A = green, B = brown) overlap partially, whereas C (krummholz, grey), and D (alpine tundra, black) provide individual groups showing a small overlap only (confidence interval = 0.95). The groups imply a very homogeneous distribution of sites, especially the group of sites D where six sites are virtually equal (black dots in the upper left corner of Fig. 6a). With regard to exposition, no major differences occur between the sites of the altitudinal transects NE and NW (Fig. 6b).

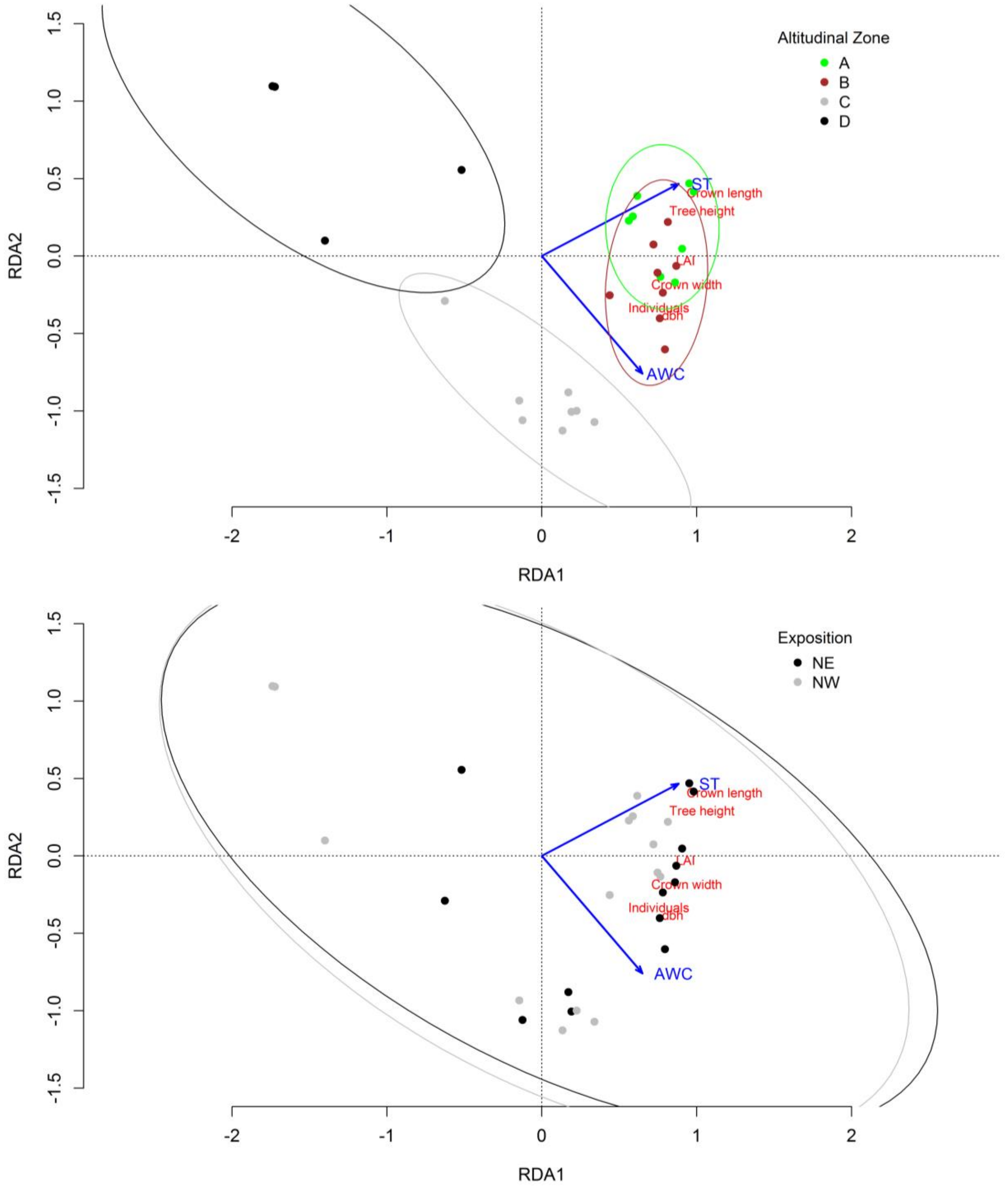

FIGURE 6. Results from *Redundancy Analysis* (RDA) with regard to altitudinal zones (a), and exposition (b). Blue arrows represent the independent explanatory variables soil temperature (ST), and available water capacity (AWC) gained as best explained principal components from preceding *Principal Component Analysis* (PCA). The dependent response variables diameter in breast height (dbh), leaf area index (LAI), tree height, crown width, crown length, and number of tree individuals (Individuals) are colored in red. Circles combine related groups of sites (NE = Northeast, NW = Northwest. A, B, C, D = Altitudinal zones). Scaling = 2 (in programming language R).

A summary of the RDA using the *RsquareAdj* function in R showed that the proportion of the total variance explained by the independent variables is 16.5%. We used the same function to see the variation explained by the individual independent variables. Hereafter, the conditional effect of ST on the dependent variables was highest (6.9%), followed by AWC (3.7%). The shared variation of the two variables was 5.9%. An *ANOVA* of the RDA results returned a *Monte Carlo permutation test* of the predictor effect, which was significant (p = 0.01).

To verify these results, and to explain the effects of each independent variable on the individual dependent variables more detailed, we separately applied a multivariate linear regression analysis with ensuing *MANOVA*. The results (Table 4a) show that the variances of the dependent variables LAI, crown width, crown length, and tree height are best explained by ST at a significance level of p = 0.05, respectively. In summary, our model for multivariate linear regression (after *MANOVA*) was significantly for ST only (p = 0.04).

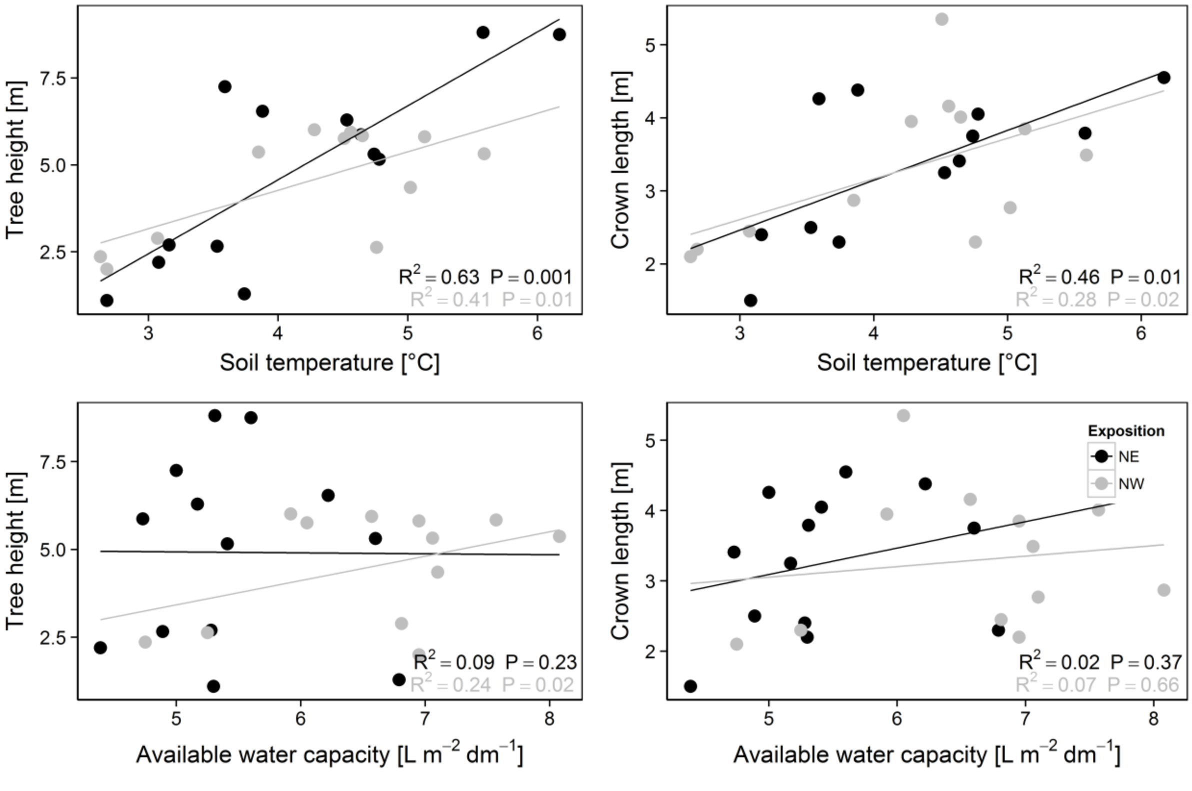

FIGURE 7. Scatter plot matrices showing simple linear regressions (R^2, P value) between soil temperature (ST) and available water capacity (AWC), respectively, and tree height and crown length, respectively, with regard to exposition. NE = Northeast, NW = Northwest, m = meter, L m^{-2} dm^{-1} = liter per square meter per decimeter.

Figure 7 illustrates the linear relationships between ST and AWC, and relevant dependent variables (tree height, crown length) with regard to exposition (NE, NW). STs were found to be significantly positive related to both tree height and crown length on NE and NW, respectively. AWC was significantly positive related to tree height on NW. No significant relations were detected between AWC and crown length (Fig. 7).

In turn, we also tested the relations between various environmental variables and the dependent variables ST, AWC, and SM with multivariate linear regression analyses. The results indicate that all three dependent variables together are best predicted by elevation ($p = 0.002$), and tree height ($p < 0.01$), where elevation explained 79 % of the variance in tree height. With regard to each individual dependent variable (Table 4b) the results were similar. Our model for the explanation of ST fitted best for tree height with an adjusted R^2 of the model of 13 % (significant, $p = 0.02$). AWC was more related to elevation, and tree height, respectively (adj. $R^2 = 44$ %, $p < 0.001$). The results for SM looked similar, with the independent variables elevation, tree height, and number of tree individuals creating the best fitting model (adj. $R^2 = 38$ %, $p < 0.001$). Neither soil-related independent variables (texture, bulk density, thickness of litter layer) nor aspect did improve the models.

TABLE 4 Results of multivariate linear regression analyses. (a) t and p values (T-test) are presented for relations between explanatory variables (ST, AWC), and response variables. The explanation of the response variables is significant at a significance level of p = 0.05. (b) The best model for explanation of the response variables (ST, AWC, SM) was produced by stepwise selection of independent variables. The results are highly significant at a significance level of p = 0.001 and p = 0.01, and significant at p = 0.05.

(a)	LAI		dbh		Tree height		Crown length		Crown width		Tree individuals	
	t	p	t	p	t	p	t	p	t	p	t	p
ST	1.72	0.05*	1.37	0.18	2.13	0.04*	2.56	0.02*	1.66	0.05*	1.21	0.24
AWC	1.09	0.29	1.21	0.24	1.02	0.32	1.15	0.26	1.20	0.24	1.07	0.30

(b)	ST				AWC				SM		
	t	p	Adj. R^2		t	p	Adj. R^2		t	p	Adj. R^2
Tree height	2.38	0.02*	0.13	Elevation	4.74	< 0.001***	0.44	Elevation	4.40	< 0.001***	0.38
				Tree height	3.40	0.002**		Tree height	3.85	< 0.001***	
								Individuals	1.96	0.05*	

Significance codes: 0.001 ‘***’, 0.01 ‘**’, 0.05 ‘*’, 0.1 ‘.’

Discussion

ST is expected to be the second most important factor controlling tree growth at its upper limit both at global and local scales (Müller et al. 2016), and multivariate statistical analyses in Rolwaling imply a significant interaction between ST and vegetation patterns as well. In fact, STs in Rolwaling indicate a significant decline with elevation, and hereby especially at the transition from the uppermost closed forest (B) to krummholz (C) (equal to timberline resp. treeline in this case). The reason why our statistical analyses did not result in a significant relation between STs and elevation (cf. Table 4b), is because year-round higher STs in the alpine tundra compared to krummholz on NE (cf. Fig. 4, Table 1). This suggests a stronger influence of solar radiation in this zone, and points to the effect of dense canopies preventing soil heat flux and radiative warming particularly underneath krummholz (cf. Aulitzky, 1961; Körner, 1998a, 1998b; Körner and Paulsen, 2004). Differences in the canopy cover are confirmed by substantially higher LAI values in the krummholz zone than in the alpine tundra (Table 3). This was also found on NW where the canopy was generally less dense (lower LAI) compared to NE along the entire transect (Table 3). However, we found different ST patterns on NW, where STs in the alpine tundra were generally lowest compared to lower elevation throughout the entire measurement period, except for autumn 2013 and winter 2013/14. This suggests that -despite a less dense canopy on NW- the influence of solar radiation is lower than on NE. Since mean STs at treeline during growing seasons in 2013, 2014, and 2015 were slightly higher or same on NW than on NE (cf. Fig. 3) –despite a lower elevation of treeline of c. 100 m-, we assume that STs alone are not responsible for the elevational position of the treeline in the study area. Moreover, the higher growing season mean ST at treeline of 7.5 ± 0.6°C compared to a suggested global mean of 6.4 ± 0.7°C (Körner, 2012) may indicate that a combination of different factors (e.g. soil water availability, soil nutrient availability) limits tree growth (e.g. Leuschner, 1996; Harsch and Bader, 2011). It has been suggested that warmer treelines are governed by seedling survival rather than growth (cf. Harsch and Bader, 2011), since seedlings are said to depend strongly on water and nutrient availability, frost damage, or are intolerant to sun exposure (Ball et al., 1991; Germino et al., 2002; Gieger and Leuschner, 2004; Holtmeier and Broll, 2005, 2007;

Smith et al., 2009). However, a c. 100 m higher position of uppermost trees on NE suggests that STs favor tree growth depending on the exposition. A higher solar radiation load finds expression in seasonal higher STs, and thus in higher trees, a thicker dbh, and a higher LAI on NE (cf. Tables 1, 3). Nevertheless, exposition as independent variable does not explain ST patterns in our statistical analyses. Also, simple linear regression analyses show no major differences in the relationships between ST, and relevant vegetation variables (tree height, crown length) with regard to the exposition (Fig. 7). Overall, our results reveal a complex microclimatic pattern of STs, which may be caused by topography-induced higher solar radiation load, and thus higher STs, and also by the vegetation pattern itself, which influences soil climatic conditions inside and outside of the closed forest resp. krummholz in different ways by shading effects and variation in leaf fall.

In contrast, the results of multivariate analyses do not show a significant impact of AWC (0-10 cm soil depth) on vegetation patterns (cf. Table 4a). In turn, SM and AWC are likely controlled by tree height and elevation (Table 4b; cf. Fig. 7), and AWC is additionally related to the number of tree individuals (Table 4b). Since elevation resp. altitude as environmental variable cannot explain differences in soil moisture (Körner, 2012) we do not attach too much importance to elevation as explanatory factor for SM resp. AWC in this analysis. Moreover, SM resp. AWC are controlled by the stand structure and the tree physiognomy themselves. Year-round lowest AWC in the alpine tundra on both transects (cf. Fig. 5, Table 2) is most likely critical in preventing seedlings from invading such sites. In the study area, Schickhoff et al. (2015) found the abundance of young growth from species *Abies spectabilis*, *Betula utilis*, and *Rhododendron campanulatum* over almost all size classes to be significantly correlated to SM. The main reasons for overall low water-holding capacities of soils in the study area are rapidly draining sandy substrates (cf. Table 3), low bulk densities (~ 1 g cm^{-3}, cf. Table 3), and a large amount of skeleton (up to 95 %), and thus a pronounced water percolation from topsoil to subsoil. This process is evidenced by well-shaped horizontal structures of soils, marked by thick (up to 30 cm) ash-grey eluvial horizons (Ae), and illuvial horizons (Bh, Bs) in the subsoil. These structures result from a soil downwards dislocation of soil organic matter, and sesquioxides (e.g. Al, Fe) with percolating water (podzolisation). In the alpine tundra, SM conditions, and also water potential in plants are both most likely additionally affected by evapotranspiration provoked by a stronger influence of both solar radiation and wind compared to forest resp. krummholz sites, resulting in an enhanced drying of topsoils and plants. Compared to forest sites, desiccation of topsoils through solar radiation and wind is strengthened by a less developed organic layer (litter layer < 0.5 cm) (cf. Wardle, 1968; Doležal and Šrutek, 2002). Likewise, tree regeneration has been observed being strongly hindered by excessive solar radiation and water stress at treelines worldwide (Aulitzky, 1960, 1961; Ferrar et al., 1988; Ball et al., 1991; Bader et al., 2007; Danby and Hik, 2007; Gill et al. 2015; Moyes et al., 2015). Overall, we assume seedling establishment in the alpine tundra in early life stages to be likely modified by SM availability, and to depend on protection from excessive solar radiation by other small growing plants (dwarf shrubs), and by topographical shelters (e.g. large rocks). Likewise, a different study in the Himalaya (Manang Valley) from Shrestha et al. (2007) showed that regeneration of *Betula utilis* is constrained by SM availability and canopy cover (light), respectively. In the same study area, *Abies spectabilis* seedling abundance has been observed to depend on SM availability and nutrients (phosphorus), respectively (Ghimire and Lekhak, 2007). Previous studies from Rolwaling indicate a significant decline of soil nutrients (e.g. nitrogen, phosphorus) along the altitudinal transects which has been interpreted as low soil nutrient availability being a most likely limiting factor for tree growth even well below the climatic treeline (Müller et al., 2016). Nutrient uptake by plants may be further affected by limited SM supply as found for other treelines as well (Loomis et al., 2006; Macek et al., 2012).

Moreover, SM is affected by low STs indirectly through freezing of soil water in the study area, predominantly in winter and spring (cf. Dong et al., 2011). Soils across the alpine treeline ecotone were frozen from October 2013 at least until end of April 2014. Higher STs (around 0°C), and higher SM resp. AWC in winter 2014/15, and spring 2015 compared to the same seasons in the previous year, suggest a thicker snow pack during these seasons. This conclusion is derived from findings that a greater snow depth usually induces warmer soils (Holtmeier and Broll, 2007, 2010; Wieser and Tausz, 2007; Hagedorn et al., 2014), leading to consistent STs around 0°C (Green, 1983; Holtmeier, 2005, 2009; Stöhr, 2007; Shi et al., 2008). In the Ural Mountains, a thicker snow cover in winter, and thus warmer soils, were found to be more important for tree growth and treeline advance than summer temperatures (Hagedorn et al., 2014). Further, a higher snow cover keeps SM high also during winter, and protects soils from frost, and small plants (dwarf scrubs and seedlings) from cold temperatures, evapotranspiration, and damage by high solar radiation and wind. In turn, a missing or thin snow cover may induce deep soil freezing (Wieser and Tausz, 2007). Thus, frost drought due to frozen soils, and mechanical damage, have been assumed to be limiting for tree growth, especially during winter months, when water uptake by plants is impeded (Larcher, 1957, 1963; Kupfer and Cairns, 1996; Oberhuber, 2004; Holtmeier, 2005; Mayr et al., 2006; Kullman, 2007). The issue of frost drought is supported by our data from winter 2013/14, and partly spring 2014 (March, April), when both STs (< 0°C) and SM were low. In contrast, winter desiccation has been negated as a cause for treeline formation (e.g. Troll, 1961; Slatyer, 1976; Körner, 1998a, 2009; Richardson and Friedland, 2009). However, late winter, and in particular spring water losses were observed not being replaced due to frozen soils and stem bases (Körner, 1998a), leading to damage of leaves/needles and branches. In the study area, winter and pre-monsoonal drought stress –in case a sufficient snow cover is missing- may not only be a problem under canopies but also in the alpine tundra, resulting in impeded tree growth and regeneration. This has been observed for several other Himalayan treelines (Schickhoff et al., 2015). It has been suggested that constraints on tree growth due to warming-related drought stress may nullify any beneficial effect on alpine treelines due to rising temperatures (González de Andrés et al., 2015).

In summary, our results show that monitoring and analyzing spatiotemporal ST and SM data over a longer period of time is valuable for a distinction of ST and SM patterns between different topographic settings, different seasons, and different years, respectively. Considering ST and SM conditions during growing season only is insufficient to understand the complex mechanisms determining the interactions between ST and SM, topography and vegetation patterns in an alpine treeline ecotone at local scales. This paper suggests an interaction of different factors (soil temperature, soil water availability, snow cover, wind, topography-induced solar radiation, vegetation, soil nutrient availability) to be responsible for tree growth and regeneration of trees in Rolwaling.

Conclusions

Our results indicate a strong interaction between STs, SM, and vegetation patterns (closed forest resp. krummholz vs. alpine tundra) in the Rolwaling treeline ecotone. We assume SM patterns to depend on alterations in snow cover, and to modify current and potential future vegetation patterns. Year-round lowest AWCs in soils of the alpine tundra are likely caused by a higher influence of solar radiation and wind compared to canopy-covered sites. We suggest seasonal drought stress in combination with nutrient-poor soils as critical factors constraining regeneration, and thus tree growth even well below the climatic treeline. Our results further show the importance of a long-term monitoring from ST and SM to determine seasonal varying soil conditions and their individual impact on vegetation patterns, tree growth, and regeneration and vice versa. With regard to the Himalaya, more studies are needed with focus on SM conditions prior to the vegetation period.

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Manuscript 3 (under review)

Soil and foliar C:N:P stoichiometry in an alpine treeline ecotone

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Keywords: carbon, C:N:P stoichiometry, P speciation in soil, Himalaya, Nepal, nitrogen, phosphorus, soil, treeline.

Abstract

Merely a few studies have addressed the soil and foliar carbon:nitrogen:phosphorus (C:N:P) stoichiometry in alpine treeline ecotones. Moreover, information on the soil nutrient availability (primarily N, P) in such ecosystems is rare. To fill these gaps, we performed a multiple data sampling in a near-natural alpine treeline ecotone in Rolwaling Himal, Nepal.

Our results show strongly varying soil C:N:P ratios and nutrient availability with soil depth. Caused by high monsoon precipitation and coarse-grained soils with low water-holding capacities, a vertical transport of nutrients and potentially mineralizable soil organic matter (SOM) in soils occurs, which is a general problem in the study area impeding growing conditions for trees. Soil N and P availability, and soil C:P and N:P ratios decrease significantly, while soil C:N ratios increase significantly as elevation increases, especially at the transition from krummholz (dominated by *Rhododendron campanulatum*) to the alpine tundra (dwarf scrub heath). These elevational trends indicate increasing nutrient (N, P) shortage especially in this area. Low N and P availability in the alpine tundra soils are likely caused by a lower litter input from dwarf shrub vegetation, and a decline in litter mineralization with elevation resulting in small accumulation of SOM. Nutrient availability in the entire study area is generally limited by low soil pH (from 2.5 to 4). In total six investigated tree species show diverse relationships between foliar and soil stoichiometric ratios, and soil nutrient availability. According to that, we assume tree growth to be rather nutrient source than sink limited, most likely due to a shortage in available N. Significantly increasing foliar C:N and C:P ratios with elevation due to significantly decreasing foliar N and P concentrations also suggest limitation in N and P. Foliar N:P ratios indicate N rather than P limitation. Contrary to previous studies from different alpine treeline ecotones, we do not consider the Rolwaling treeline ecotone as anarea of nutrient accumulation. We conclude that elevational variations in stand structures themselves govern nutrient cycling through the input of C, N, and P into soils by differences in litterfall.

Introduction

Ecological stoichiometry is a powerful indicator of diverse ecological processes such as energy flow, material cycling, and nutrient limitation across diverse ecosystems (Elser et al., 1996). In terrestrial ecosystems, the biogeochemical cycles of carbon (C), nitrogen (N), and phosphorus (P) are coupled through the biochemical reactions during primary production, respiration, and decomposition (Finzi et al., 2011). N and P are among the most important nutrients that limit plant growth and different biological processes in terrestrial ecosystems (Vitousek and Howarth, 1991; Güsewell, 2004; Reich and Oleksyn, 2004; Elser et al., 2007). Thus, the soil and foliar C:N:P stoichiometry in alpine treeline ecotones can improve our understanding of nutrient availability and their potential limitation.

Variations in soil nutrient supply to plants result from different factors such as microclimate, soil type, texture and age, and the impact of plants on SOM quality (Jenny, 1980; Vitousek et al., 1993). A major factor is low soil temperature, which slows down microbial activity and the rates of soil respiration, and thus litter decomposition including N and P mineralization (e.g. Boczulak et al., 2015). In contrast to soil N availability, soil P availability is less affected by temperature-driven biological processes but more by mechanical rock weathering (e.g. Jiao et al., 2016). Another important factor in controlling litter decomposition including N and P mineralization is soil moisture (e.g. Loomis et al., 2006; Withington and Sanford, 2007; Sardans and Peñuelas, 2012; Xiao et al., 2014), which governs microbial activity and mobilizes nutrients (e.g. Sleutel et al., 2008). Furthermore, nutrient availability is affected by physical soil properties like soil texture, and can differ widely within soil profiles depending on pedogenic processes. For instance, Podzols show a strong vertical dislocation of SOM accompanied by sesquioxides (Al-/Fe-complexes) from topsoils to subsoils (Lundström et al., 2000; Buurman and Jongmans, 2005). Podzols are usually acid soils characterized by low soil pH constraining microbial activity and the availability of soil nutrients (e.g. Khanna et al., 2007).

There is evidence that C, N, and P concentrations in soils are closely related since soil C turnover rates are commonly constrained by the soil N and P availability (e.g. Bradford et al., 2008; Manzoni and Porporato, 2009; Stottlemyer et al., 2011). According to that, soil C:N:P ratios were found to be remarkably well-constrained at different scales (e.g. Cleveland and Liptzin, 2007; Tian et al., 2010; Kirkby et al., 2011). Thus, a literature review by Cleveland and Liptzin (2007) revealed a mean soil C:N:P ratio of 186:13:1 at a global scale, however, several studies from diverse ecozones ascertained different C:N:P ratios in soils (e.g. Li et al., 2012; Zhang et al., 2013; Bing et al., 2015; Jiao et al., 2016). For example, soil C:N:P ratios were found to vary depending on existing vegetation communities, fire impact, land use, local climate (e.g. precipitation, temperature), soil depth, and soil development (Aponte et al., 2010; Li et al., 2012; Bui and Henderson, 2013; Bing et al., 2015; Jiao et al., 2016). Besides, diverse N and P fractions were used for calculating soil C:N:P ratios. Commonly, total N and P were used (e.g. Griffiths et al., 2012), however sometimes derived from different determination methods. For example, Yang and Post (2011) used the organic Hedley-P fractions (P_o) (according to Hedley et al., 1982), while Bing et al. (2015) considered total Hedley-P as well as a combination of organic and inorganic Hedley-P fractions (HCO_3^--P_i and -P_o, resin-P_i) for available P. A study by Hacker et al. (submitted) showed the strongest relationship with microbial P (as soil component relevant for stoichiometric considerations) for the sum of labile and moderately labile Hedley-P_i and -P_o fractions. The different use of P needs to be considered when interpreting and comparing results from different studies.

To date, soil nutrient availability and soil C:N:P ratios in alpine treeline ecotones are insufficiently explored. Since mountains are characterized by rapid changes in environments and vegetation communities along elevational gradients, even over short distances, similar changes in soil nutrient availability (e.g. Köhler et al., 2006; Loomis et al, 2006; Müller et al., 2016a), and soil C:N:P ratios are likely (e.g. Liptzin et al., 2012; Zhao et al., 2014). To our knowledge, only a handful of studies with the focus on soil C:N:P ratios in alpine treeline ecotones exist. Liptzin et al. (2012) ascertained accumulation of soil nutrients (C, N, P) underneath krummholz in an alpine treeline ecotone in Colorado, USA. They interpreted this as a higher importance of indirect effects of trees on soils (interactions among trees and wind) than of direct effects (vegetation type). In addition, they found both lower soil C:N and higher soil total and available N:P ratios in the alpine tundra compared to lower elevations (forest, krummholz), from which they assumed P limitation in the tundra and N limitation underneath forest and krummholz. In China, Bing et al. (2015) found significantly decreasing soil C:N ratios, and decreasing ratios of soil C and N to plant-available P and total P in varying soil depths with elevational changes in vegetation communities. However, their results showed lower or similar soil C:P and N:P ratios in the lowest parts of the subalpine forest compared to higher elevations. This was interpreted to result from a higher transformation of P by microbes combined with higher temperatures and higher litter input at lower elevations. Another study from China (Zhao et al., 2014) found overall declining soil total and available nutrient C, N, and P concentrations with elevation. In their analyses, the elevational foliar C:N:P stoichiometry patterns were stronger affected by plant growth form (herbs, shrubs, trees) than by soil or climate variables. In Austria, Huber et al. (2007) found reduced rates of

N turnover and accumulation with elevation resulting from decreasing temperatures. A decline in SOM with elevation was also reflected by decreasing soil C concentrations leading to closer soil C:N ratios (Huber et al., 2007). Alpine tundra soils were characterized as areas with low mineralization rates of SOM due to prevalent cold and dry conditions, which constrain nutrient supply, and in turn limit plant production (e.g. Bowman et al., 1993; Liptzin and Seastedt, 2009). Overall, soil C:N:P stoichiometric patterns in alpine treeline ecotones are far from being fully understood. The role of individual soil nutrients (especially N) in alpine treeline ecotones are reviewed in Müller et al. (2016a).

Apart from soils, a bulk of studies investigated foliar and also litter C:N:P ratios (e.g. Sterner and Elser, 2002; McGroddy et al., 2004; Güsewell, 2004; Reich and Oleksyn, 2004). The foliar N:P ratio of individual plant species is expected to serve as an indicator of nutrient limitation (e.g. McGroddy et al., 2004; Reich and Oleksyn, 2004; Sardans and Peñuelas, 2012; Sardans et al., 2015a, b). According to that, plants are limited in N at a foliar N:P ratio below 14, and are limited in P above 16 (Koerselman and Meuleman, 1996; Aerts and Chapin, 2000; Cleveland and Liptzin, 2007). According to Güsewell (2004), N limitation occurs at foliar N:P ratios below 10 while P limitation appears below 20. A global scale study by Reich and Oleksyn (2004) found that foliar C:N, C:P, and N:P ratios of community biomass depend on plant physiology, soil biogeochemistry, and plant community composition along latitudinal (geographic and temperature) gradients. In contrast, studies with focus on potential elevational changes in foliar stoichiometric ratios occur less frequently, and are almost completely absent with regard to alpine treeline ecotones (Zhao et al., 2014). A prominent hypothesis is that tree growth in alpine treeline ecotones is rather nutrient sink than source limited (Körner, 1998; Smith et al., 2003; Seastedt et al., 2004). The sink (growth) limitation hypothesis (Körner, 1998, 2012) implies that suppression of meristematic activity can limit tree growth directly at low temperatures when photosynthesis is not necessarily limited. In accordance with this, several studies found higher concentrations of C and N in tissues at treeline compared to lower elevations, which were said to support high metabolic activity (e.g. Weih and Karlsson, 2001; Shi et al., 2008; Fajardo et al., 2012, 2013). In contrast, the source (net photosynthesis) limitation hypothesis suggests that trees are unable to gain as much C or nutrients as they would be able to use for growth due to low nutrient availability or drought stress (Körner, 1998, 2012; Sveinbjörnsson et al., 2010). In line with this, some studies detected lower foliar N concentrations due to lower soil N availability at treeline compared to lower elevations (e.g. Köhler et al., 2006; Huber et al., 2007; McNown and Sullivan, 2013; Sullivan et al., 2015; Müller et al., 2016a). An increase in photosynthesis, and thus C assimilation can only be guaranteed by an appropriate availability of soil N, which is essential in generating high-energy compounds such as ATP and NADPH during photosynthesis. Finally, microorganisms outcompeted trees in terms of uptake of limiting soil nutrients (N) serving as a potential cause for limited tree growth in alpine treeline ecotones (Liu et al., 2012; Thébault et al., 2014).

Previous studies found a changing soil C, N, and P supply, and thus changing foliar stoichiometric ratios with altering climatic conditions such as temperature or precipitation (e.g. Walker and Syers, 1976; McGill and Cole, 1981; Reich and Oleksyn, 2004). This suggests potential shifts in the stoichiometric coupling of soil and foliar C, N, and P concentrations in alpine treeline ecotones, where climatic conditions (e.g. decreasing temperatures) are different compared to lower elevations. Alterations in the foliar C:N:P stoichiometry have been shown to be species-specific as it is inherently occurring at a global scale, i.e. some tree species show nutrient concentrations proportional to the nutrient source (stoichiometric plasticity), whereas others are characterized by consistently regulated nutrient concentrations independent of changing soil nutrient availability (stoichiometric homoeostasis) (Sterner and Elser, 2002; Zhang et al., 2013; Sardans et al., 2015a). These relationships were expressed in the T-Biogeochemistry hypothesis (Reich and Oleksyn, 2004), which stated that the soil nutrient availability depending on temperatures has effects on the foliar nutrient concentrations. Thus, individual species may react in different ways to potential elevational changes in soil nutrient availability and soil stoichiometry at a local scale. With regard to alpine treeline ecotones, these processes are not well explored.

In this paper, we hypothesize that

(i) decomposition of soil organic matter (SOM) decreases with elevation due to lower soil temperatures. Consequently, this results in higher soil C concentrations, and wider C:N and C:P_o ratios compared to lower elevations due to a decrease in C respiration losses. Furthermore, lower decomposition at higher elevations leads to less mineralization of N, and thus lower soil N availability. The generally low soil P availability (P_{av}) is provided predominantly by mineralization at lower elevations, while mechanical rock weathering prevails at higher elevations. Thus, no elevational effects are expected. Resulting from this, the soil N_{min}:P_{av} ratios decrease with elevation, while soil N:P_o ratios most likely remain constant since both are governed by mineralization.

(ii) tree growth declines with elevation, because the ability of trees to use available C is limited due to nutrient shortage and changing environmental conditions (e.g. lower soil temperatures). Sink limitation is reflected by an accumulation of C in tissues to compensate the lower demand on growth. According to that, foliar C:N and C:P ratios increase with elevation. Because of lower soil N availability with elevation, the limitation in N increases, and thus foliar N:P ratios decrease with elevation.

(iii) SOM originates from plant litter. During mineralization of SOM and respiration of heterotrophs a loss in C occurs, leading to generally closer C:N ratios. Since the mineralization of litter decreases with elevation, the relationships between soil C:N and litter C:N ratios become closer compared to lower elevations. Furthermore, the availability of soil nutrients controls tree growth limitation. Thus, foliar N:P ratios are related to N_{min}, P_{av}, and N_{min}:P_{av} ratios.

Materials and methods

Study area and experimental design

The Rolwaling valley is located in the northeast part of Central Nepal (N 27°54’, E 86°22’; Fig. 1a). The experimental area is situated on the unsettled north-exposed slope opposite to the village of Beding. A stratified random experimental design was used with three transects (NE1 = Northeast 1, NW1 = Northwest 1, NE2 = Northeast 2; Figs. 1a, b) across the treeline ecotone divided into four altitudinal zones: A (closed subalpine forest), B (uppermost subalpine closed forest), C (krummholz), and D (dwarf scrub heath or alpine tundra; Figs. 1a, b). Within each zone of each altitudinal transect, four different experimental plots (20 m x 20 m; projected on a horizontal plain) were randomly selected (Figs. 1a, b). The transect NW1 had two additional plots in altitudinal zone A.

Subalpine forests are primarily composed of *Abies spectabilis* (*Abies*) and *Betula utilis* (*Betula*), with *Acer caudatum* (*Acer*), *Rhododendron campanulatum* (*Rhc*), and *Sorbus microphylla* (*Sorbus*) forming a second tree layer (Schickhoff et al., 2015; Schwab et al., 2016). Upslope, the forests convert into an extensive krummholz belt of *Rhc* (ca. 3900 m a.s.l., NW exposition; ca. 4000 m a.s.l., NE exposition), which turns into alpine *Rhododendron anthopogon* and *Rhododendron setosum* (*Rhas*) dwarf scrub heaths at ca. 4000 m a.s.l. and 4100 m a.s.l., respectively. Dwarf shrubs are interspersed by low growing individuals (diameter in breast height (dbh) < 7 cm) or young growth of *Abies*, *Betula*, and *Rhc*. Here, scattered *Sorbus* individuals with dbh ≥ 7 cm occur (Schwab et al., 2016). Ground cover vegetation and species richness decrease from the closed subalpine forests across the treeline ecotone (Schwab et al., 2016). The occurring tree and shrub species are prevailing shallow rooting plants (ca. 0-20 cm, own observations).

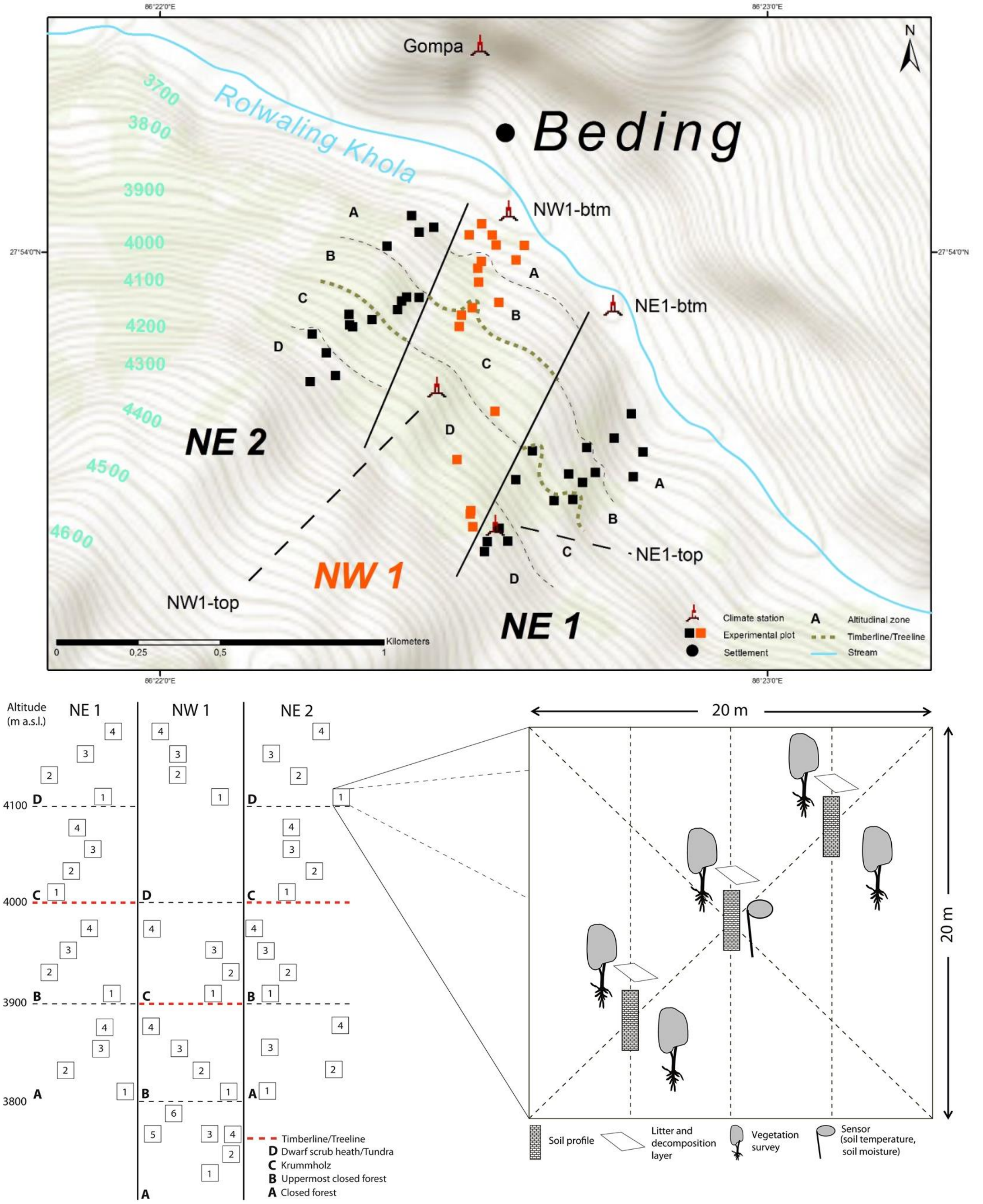

Figure 1. Study area and experimental design (a) including topography, location of the altitudinal zones (A, B, C, D) and experimental plots as part of three altitudinal transects (NE1 = Northeast 1, NW1 = Northwest 1, NE2 = Northeast 2), and location of the climate stations (btm = bottom, top). (b) Schematic illustration of the three altitudinal transects including four experimental plots (20 m x 20 m) respectively in each altitudinal zone (left). Plot design is equivalent on each plot (right). The altitudinal transects in (a), and (b) (left) are mirror-inverted.

Due to isolation and a very low population density of the Rolwaling valley, and virtually pristine vegetation, the treeline ecotone is considered as near-natural (Schwab et al., 2016). Based on measurements of atmospheric N deposition (NO_2, NH_3) using passive devices (Passam Inc., Switzerland) no input of atmospheric N derived from human activities occurred. Bedrock is granite and gneiss, containing a low proportion of P (< 0.2 mass% P_2O_5). Soils were classified as Podzols (IUSS, 2006), characterized by coarse-grained (sandy) soil texture, and a substantial outwash of SOM and sesquioxides from topsoils to subsoils (podsolization). Soils had generally low pH, increasing slightly with soil depth (from 2.5 to 4). Podzols showed the typical sequence of Oi-Oe-Ah-Ae-Bh-Bs.

Climate in the study area is characterized as warm temperate with cool summers and dry winters. From June to September, it is intensively affected by the South-Asian summer monsoon accounting for more than 70% of the annual precipitation. In 2014, four automatic climate stations (HOBO U30-NRC; ONSET Computer Corporation, USA) measured mean annual air temperatures from 3.6°C at the valley bottom (NE1-btm, NW1-btm; Fig. 1a) to 2.9°C (NW1-top) and 2.8°C (NE1-top) in the alpine tundra (cf. Gerlitz et al., 2016). Annual precipitation sums were 1042 mm (NE1-btm), 1046 mm (NW1-top), 1161 mm (NW1-btm), and 1316 mm (NE1-top). In 2014, modified soil sensors (koubachi Inc., Switzerland) measured mean soil temperatures of 3.07°C (zone A), 4.08°C (zone B), 2.28°C (zone C), and 3.16°C (zone D) on the NE2 transect. Along the NW1 transect, mean soil temperatures were 3.46°C (A), 3.85°C (B), 2.36°C (C), and 2.00°C (D) (cf. Müller et al., 2016b). Mean soil moisture (expressed as available water capacity in L m^{-2} dm^{-1}) decreased significantly on both transects (NE2: A = 5.20, B = 5.17, C = 5.02, D = 4.88; NW1: A = 6.84, B = 6.27, C = 5.66, D = 5.22).

Soil and biomass data collection

Three soil profiles were surveyed on each of the 50 experimental plots (Figs. 1a, b) according to Ad hoc-Arbeitsgruppe Boden (2005). From these profiles the respective mineral soil horizons (Ah, Ae, Bh, Bs) were combined to composite samples. Further, three organic layer samples of each the Oi and Oe layers were collected. Moreover, foliage of the living evergreen tree species *Abies* and *Rhc* as well as the evergreen shrub species *Rhas* were sampled above the soil profiles. Sampling took place at the onset of May 2013 and 2014, and in September 2014 and 2015. Additionally, the deciduous tree species *Acer*, *Betula*, and *Sorbus* were sampled in September 2014 and 2015. The years 2013, 2014, and 2015 were normal years with regard to weather conditions (own data derived from the climate stations in the study area; Fig. 1a).

Soil samples were analyzed for total carbon (C), total nitrogen (N), plant-available nitrogen (N_{min}), total phosphorus (P), plant-available phosphorus (P_{av}), and pH. Total C concentrations are equal to soil organic carbon (C_{org}). C and N concentrations of soils, organic layers, and foliage were determined using an elemental analyzer (vario EL II; elementar, Germany). For analysis of soil N_{min} (NO_3^-, NH_4^+), an aliquot of 10 g of homogenized field-fresh soil material with 1 M KCl solution was shaken rigorously every 15 minutes for one hour. The extraction solution was filtered, and acidified with HCl, subsequently. N_{min} fractions were analyzed in the laboratory by continuous flow analysis (CFA, SEAL Auto Analyzer AA3 HR; SEAL Analytical Inc., UK). Total P and plant-available P of soil samples were assessed following a modified protocol of Hedley et al. (1982). The sequential extraction of P was reduced to four steps where the extracted fractions comprised 0.5 M $NaHCO_3$-P_i and -P_o (labile), 0.1 M NaOH- P_i and -P_o (moderately labile), 1 M concentrated HCl-P, and 0.5 M H_2SO_4-P (both stable). In each extraction solution, inorganic P fractions (P_i) were measured with CFA, and organic P fractions (P_o) with ICP-OES (Perkin Elmer Optima 5300 DV; Perkin Elmer, USA). A study by Hacker et al. (submitted) showed the strongest relationship with microbial P (as soil component relevant for stoichiometric considerations) for the sum of labile and moderately labile P_i and P_o concentrations (in this study expressed as P_{av}). pH of soils was measured 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; WTW Inc., Germany). Besides, litter and foliage were investigated for total P (expressed per unit of dry biomass, mg g^{-1}) by measuring with ICP-OES after microwave-digestion (MLS START 1500 Microwave Extractor; EVISA, Germany; application E208 - plants low acidity: 4 ml HNO_3, 3 ml H_2O_2, 5 ml H_2O).

Statistical analyses

Statistical analyses were conducted using the free programming language R, version 3.1.2 (R Development Core Team, 2014) by applying the R-packages *car* (Fox and Weisberg, 2011), *MASS* (Venables and Ripley, 2002), *PMCMR* (Pohlert, 2014), and *stats* (R Development Core Team, 2014). Data was log transformed to improve normality and homogeneity of variance. The reported means and standard errors are the back transformed values. We tested potential significant ($P < 0.05$ hereafter) differences among the altitudinal zones in soil and foliar C, N, and P concentrations, soil and foliar C:N:P ratios, and soil N and P availability using a one-way ANOVA or a Kruskal-Wallis test depending on the Gaussian distribution and homogeneity of variance of the data. The significance of differences was examined by applying a Post hoc Tukey HSD test or a Post hoc Nemenyi (Tukey) test. We further tested for potential changes in soil and foliar element concentrations and their ratios with elevation [m a.s.l.] using the Spearman correlation analysis and linear regression. To test the relationships between soil stoichiometry (C:N, C:P, N:P) or soil nutrient availability (Nmin, Pav), and foliar stoichiometry (C:N, C:P, N:P), also with regard to altitudinal variations in stand structures, multiple and bivariate linear regression analyses were performed. We chose topsoil variables, since it was the largest dataset, and the tree and shrub species mainly root in this part of the soils. The multiple analyses included stepwise backward regression, where the variables were excluded stepwise from the analyses that did not contribute significantly to the explained variation. This method was applied to the six species *Abies, Acer, Betula, Rhas, Rhc,* and *Sorbus* separately.

Results

Soil N and P availability

Plant-available soil Nmin, and Pav concentrations [mg kg^{-1}] varied with altitudinal changes in stand structures (Tables 1, 2; see Appendix Fig. S1b in online supplementary data), and distinctly with soil depth (Table S1; Fig. S1a, b).

We found significantly negative correlations between topsoil Nmin concentrations and elevation [m a.s.l.], irrespective of the year (May 2014: r = -0.66; Sep 2014: r = -0.45; Sep 2015: r = -0.58). A one-way ANOVA resulted in significant differences of topsoil Nmin concentrations between the subalpine forest (zones AB), and krummholz (C) and alpine tundra (D) (Tables 2, S1). We also found a significant decline in topsoil Pav concentrations with elevation [m a.s.l.] (May 2013: r = -0.46; May 2014: r = -0.61). Differences in the topsoil Pav concentrations among the subalpine forest (zones AB), and krummholz and alpine tundra (CD) were less pronounced (Tables 1, 2), but significant.

Soil C:N:P stoichiometry

The total concentrations of C, N, and P, and their ratios changed considerably with soil depth across the entire treeline ecotone (Table S3; Figs. S1a, b). The highest total C, N, and P concentrations were found in both organic layers (Oi, Oe; for C and N see Müller et al., 2016a). In May 2013, mean soil C:N:P ratios in the study area differed significantly from 370:19:1 (topsoils) to 196:10:1 (Ae), 283:12:1 (Bh), and 221:9:1 (Bs) (Table S3). In the following year (May 2014), we found significant differences in mean soil C:N:P ratios from 457:23:1 (topsoils), 228:11:1 (Ae), 278:12:1 (Bh), and 235:9:1 (Bs) (Table S3). Topsoil C:N ratios were remarkably consistent during all of the four sampling dates (Table S2).

We detected significant correlations between elevation [m a.s.l.] and topsoil N concentrations (May 2013: r = -0.49; May 2014: -0.63; Sep 2014: -0.60; Sep 2015: -0.65), topsoil C:N ratios (0.81; 0.64; 0.72; 0.82), and topsoil total P concentrations (May 2013: -0.49; May 2014: -0.33). For topsoil C concentrations, C:P, C:P_o, N:P, and N:P_o ratios no significant relationships with elevation [m a.s.l.] were detected.

Topsoil total C and N concentrations were similar in the subalpine forest (zones AB) and krummholz (C), but were significantly different in the alpine tundra (D) at all sampling dates (Tables 2, S2). Topsoil total P concentrations varied significantly between the zones A, BC, and D (Table 1). Topsoil C:N ratios were significantly different between the zones AB and CD at all sampling dates (Tables 2, S2), while topsoil C:P and C:P_o ratios increased from the zones AB to C, but decreased significantly in D (Table 2). Topsoil N:P and N:P_o ratios were similar in the zones ABC, and differed significantly in D (Table 2). We found very low N_{min}:P_{av} ratios between 0.02 and 0.1, and N_{min}:$NaHCO_3$-P_i ratios between 0.5 and 3 (Table 2). Significant differences for these ratios occurred between altitudinal zones AB and CD (Table 2).

Figure 2 shows the relationships between topsoil and litter (O_i) C:N ratios with regard to the different altitudinal zones. The relations became closer with altitudinal changes in stand structures, which were expressed by increasing coefficients of determinations from the uppermost subalpine forest (zone B; $R^2 = 0.26$), to krummholz (C; $R^2 = 0.39$), to the alpine tundra (D; $R^2 = 0.75$). In general, the thickness of the organic layer O_i decreased significantly (r = -0.71) with elevation [m a.s.l.], and differed significantly between ABC and D.

Table 1. Topsoil P fractions [mg kg^{-1}] in the altitudinal zones A (subalpine forest), B (uppermost subalpine forest), C (krummholz), and D (alpine tundra). Values result from a sequential Hedley P fractionation (according to Hedley et al., 1982) in May 2013 and 2014.

	Zone	**$NaHCO_3$-Pi**	**$NaHCO_3$-Po**	**NaOH-Pi**	**NaOH-Po**	**HCl-P**	**H_2SO_4-P**	**Total P**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	**Mean ± s.e.**
May 2013	A *(14)*	51.10 ± 38.47 ^{a}	155.10 ± 56.78 ^{a}	78.25 ± 25.84 ^{a}	461.38 ± 129.63 ^{a}	58.93 ± 15.74 ^{a}	45.83 ± 16.02 ^{a}	**846.33 ± 204.10 ^{a}**
	B *(12)*	69.92 ± 37.39 ^{a}	84.16 ± 33.84 ^{b}	90.29 ± 29.15 ^{a}	376.85 ± 118.32 ^{ab}	62.20 ± 16.63 ^{a}	40.70 ± 9.92 ^{a}	**724.12 ± 176.68 ^{b}**
	C *(12)*	53.92 ± 31.97 ^{a}	83.88 ± 51.07 ^{b}	60.14 ± 14.90 ^{b}	330.26 ± 82.00 ^{b}	47.96 ± 8.49 ^{a}	45.90 ± 17.82 ^{a}	**622.07 ± 110.90 ^{b}**
	D *(10)*	46.19 ± 34.22 ^{a}	94.85 ± 32.53 ^{b}	80.20 ± 32.77 ^{a}	272.87 ± 74.69 ^{b}	72.08 ± 47.38 ^{a}	29.61 ± 16.73 ^{a}	**595.80 ± 150.36 ^{c}**
May 2014	A *(14)*	60.94 ± 44.46 ^{a}	98.07 ± 33.98 ^{a}	84.23 ± 25.05 ^{a}	371.53 ± 120.42 ^{a}	58.97 ± 19.73 ^{a}	53.09 ± 35.06 ^{a}	**726.83 ± 225.00 ^{a}**
	B *(12)*	45.34 ± 32.60 ^{ab}	82.79 ± 40.60 ^{a}	70.33 ± 17.22 ^{a}	314.67 ± 74.53 ^{a}	53.27 ± 15.56 ^{a}	52.94 ± 43.48 ^{a}	**619.36 ± 179.25 ^{b}**
	C *(12)*	40.03 ± 32.56 ^{ab}	84.66 ± 48.36 ^{a}	65.11 ± 35.86 ^{a}	310.15 ± 112.05 ^{a}	43.29 ± 10.02 ^{a}	68.69 ± 32.83 ^{a}	**611.92 ± 221.32 ^{b}**
	D *(12)*	22.58 ± 15.00 ^{b}	90.59 ± 26.99 ^{a}	64.63 ± 14.19 ^{a}	313.06 ± 86.98 ^{a}	54.05 ± 17.77 ^{a}	48.57 ± 27.06 ^{a}	**593.48 ± 121.14 ^{c}**

Values are means ± standard error (s.e.); different letters between four items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.* $NaHCO_3$ = bicarbonate; SOC, NaOH = hydroxide; HCl = hydrochloric acid; H_2SO_4 = sulfuric acid; Pi = inorganic P fractions; Po = organic P fractions; P = phosphorus.

Table 2. Topsoil C, N, P_{av}, P_o [mg g^{-1}], and N_{min} [mg kg^{-1}] concentrations, and topsoil C:N, C:P, C:Po, N:P, N:P_o, N_{min}:P_{av} and N_{min}:$NaHCO_3$-Pi ratios in altitudinal zones A (subalpine forest), B (uppermost subalpine forest), C (krummholz), and D (alpine tundra).

	Zone	**C [mg g^{-1}]**	**N [mg g^{-1}]**	**Nmin [mg kg^{-1}]**	**Pav [mg g^{-1}] ***	**Po [mg g^{-1}] ***	**C:N**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
May 2013	A *(14)*	204.20 ± 84.82 ^{a}	12.11 ± 5.49 ^{a}	no data	0.74 ± 0.18 ^{a}	0.62 ± 0.17 ^{a}	17.22 ± 1.15 ^{a}
	B *(12)*	235.01 ± 67.79 ^{a}	12.98 ± 3.37 ^{a}	no data	0.62 ± 0.16 ^{a}	0.46 ± 0.15 ^{b}	18.27 ± 2.59 ^{b}
	C *(12)*	245.10 ± 73.91 ^{a}	11.41 ± 3.25 ^{a}	no data	0.53 ± 0.10 ^{b}	0.41 ± 0.09 ^{b}	21.39 ± 1.59 ^{c}
	D *(10)*	171.02 ± 70.10 ^{b}	7.39 ± 3.58 ^{b}	no data	0.49 ± 0.15 ^{b}	0.37 ± 0.10 ^{b}	22.59 ± 2.37 ^{c}
May 2014	A *(14)*	240.95 ± 96.67 ^{a}	13.99 ± 5.56 ^{a}	44.70 ± 35.66 ^{a}	0.61 ± 0.18 ^{a}	0.46 ± 0.14 ^{a}	17.26 ± 1.46 ^{a}
	B *(12)*	244.36 ± 101.80 ^{a}	12.44 ± 4.66 ^{a}	46.25 ± 37.89 ^{a}	0.54 ± 0.13 ^{a}	0.40 ± 0.11 ^{b}	19.40 ± 1.77 ^{a}
	C *(12)*	274.44 ± 107.70 ^{a}	12.05 ± 4.13 ^{ab}	18.16 ± 13.70 ^{b}	0.50 ± 0.20 ^{b}	0.39 ± 0.16 ^{b}	21.52 ± 2.91 ^{b}
	D *(12)*	180.92 ± 76.27 ^{b}	8.35 ± 2.81 ^{b}	12.17 ± 7.55 ^{c}	0.48 ± 0.10 ^{b}	0.43 ± 0.11 ^{b}	21.61 ± 2.63 ^{b}

		C:P *	**C:Po ***	**N:P ***	**N:Po ***	**Nmin:Pav ***	**Nmin:$NaHCO_3$-Pi ***
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
May 2013	A *(14)*	286.91 ± 68.47 ^{a}	353.53 ± 108.72 ^{a}	16.90 ± 4.33 ^{ab}	20.82 ± 6.60 ^{a}	no data	no data
	B *(12)*	392.55 ± 91.32 ^{ab}	541.97 ± 134.96 ^{ab}	21.24 ± 5.44 ^{a}	29.19 ± 7.09 ^{b}	no data	no data
	C *(12)*	470.24 ± 135.92 ^{b}	620.52 ± 208.42 ^{b}	21.71 ± 5.83 ^{a}	28.67 ± 9.08 ^{b}	no data	no data
	D *(10)*	330.96 ± 131.09 ^{a}	437.93 ± 162.99 ^{a}	14.62 ± 5.58 ^{b}	19.28 ± 6.82 ^{a}	no data	no data
May 2014	A *(14)*	395.54 ± 92.21 ^{a}	520.86 ± 140.17 ^{a}	22.80 ± 4.59 ^{a}	30.02 ± 7.46 ^{a}	0.06 ± 0.04 ^{a}	0.95 ± 0.60 ^{a}
	B *(12)*	470.82 ± 131.31 ^{ab}	606.69 ± 147.13 ^{ab}	24.10 ± 5.57 ^{a}	31.23 ± 6.94 ^{a}	0.08 ± 0.04 ^{a}	1.17 ± 0.88 ^{a}
	C *(12)*	589.90 ± 256.08 ^{b}	753.25 ± 335.42 ^{b}	25.82 ± 8.28 ^{a}	32.88 ± 12.12 ^{a}	0.04 ± 0.03 ^{b}	0.66 ± 0.57 ^{b}
	D *(12)*	348.15 ± 172.26 ^{a}	427.93 ± 190.92 ^{a}	15.52 ± 5.90 ^{b}	19.13 ± 6.77 ^{b}	0.02 ± 0.01 ^{b}	0.55 ± 0.34 ^{b}

Values are means ± standard error (s.e.); different letters between four items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.* No data = no data available. *As soil component relevant for stoichiometric considerations, the sums of $NaHCO_3$- and NaOH-P-fractions (P_{av}), and of $NaHCO_3$- and NaOH-P_o (P_o), and $NaHCO_3$-Pi were used for P.

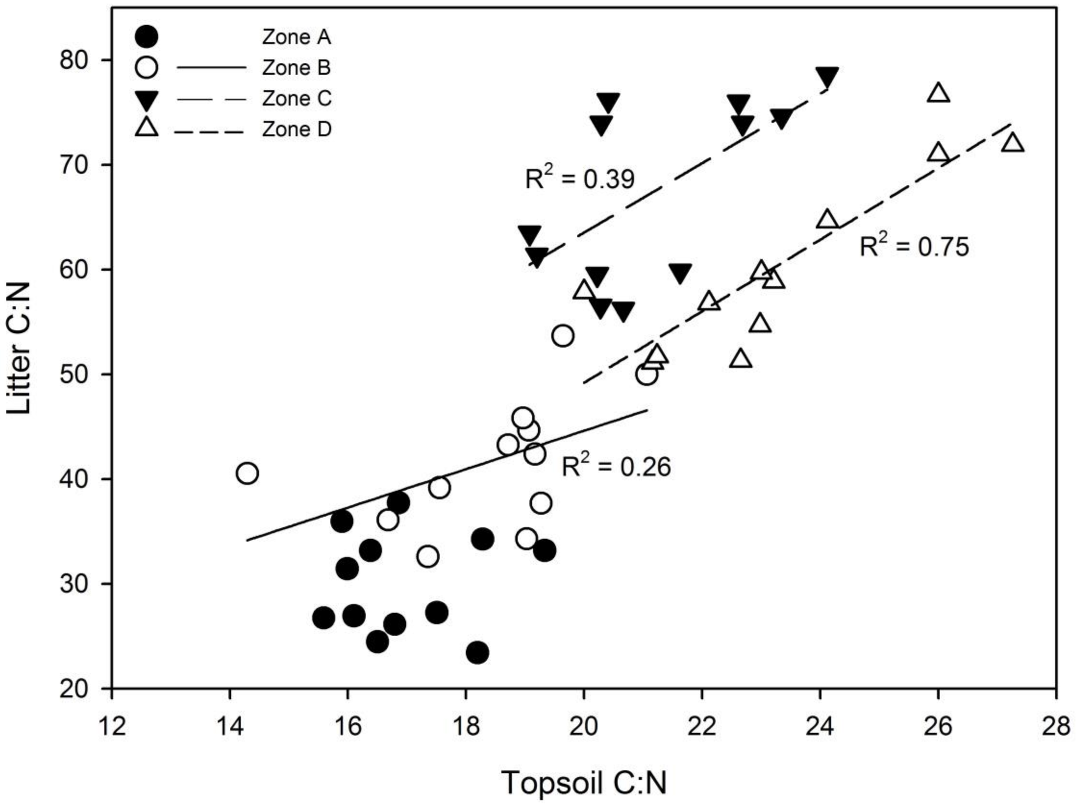

Figure 2. Relationships between topsoil (Ah) and litter (Oi) C:N ratios with respect to the different altitudinal zones A (subalpine forest; filled dots), B (uppermost subalpine forest; white dots), C (krummholz; filled triangles), and D (alpine tundra; white triangles). Data originates from May 2013. Lines with R^2 indicate significant linear regressions at $P < 0.05$. No significant relationship was found in the subalpine forest (A).

Foliar C:N:P stoichiometry

The foliar C:N:P stoichiometric ratios were species-specific throughout the treeline ecotone. An ANOVA testing the differences between the six investigated species resulted in two different groups of species. Foliar C:N and C:P ratios in three evergreen species *Abies*, *Rhc*, and *Rhas* varied significantly from foliar C:N and C:P ratios in the three deciduous tree species *Acer*, *Betula*, and *Sorbus* (September 2014, 2015). However, the analyses did not show significant variations in foliar N:P ratios. Overall, we found the following mean foliar C:N:P ratios in the evergreen species: *Rhc* (May 2013: 433:12:1; May 2014: 404:12:1; Sep 2014: 371:14:1; Sep 2015: 381:12:1), *Abies* (414:12:1; 404:12:1; 304:12:1; 322:11:1), *Rhas* (405:12:1; 416:12:1; 442:14:1; 403:12:1). The mean foliar C:N:P ratios in the deciduous species were: *Acer* (Sep 2014: 199:12:1; Sep 2015: 206:11:1), *Betula* (234:11:1; 226:12:1), *Sorbus* (230:9:1; 281:11:1).

Furthermore, foliar C:N:P stoichiometry varied with altitudinal changes in stand structures (Tables 3, S4-S8). Likewise, the six investigated species showed diverse trends in foliar nutrient concentrations with elevation [m a.s.l.] (Fig. 3). Foliar C concentrations in the evergreen species *Abies*, *Rhc*, and *Rhc* were not significantly related to elevation [m a.s.l.] nor did they differ between the altitudinal zones (Tables 3, S4, S8). Foliar C concentrations in deciduous *Sorbus* increased significantly with elevation [m a.s.l.] (Fig. 3), and also differed significantly between the subalpine forest (zones AB), and krummholz and the alpine tundra (CD) (Table S5). In deciduous *Acer*, foliar C concentrations decreased significantly with elevation [m a.s.l.] (Fig. 3), and also varied significantly between the zones AB and C (Table S6) in September 2015.

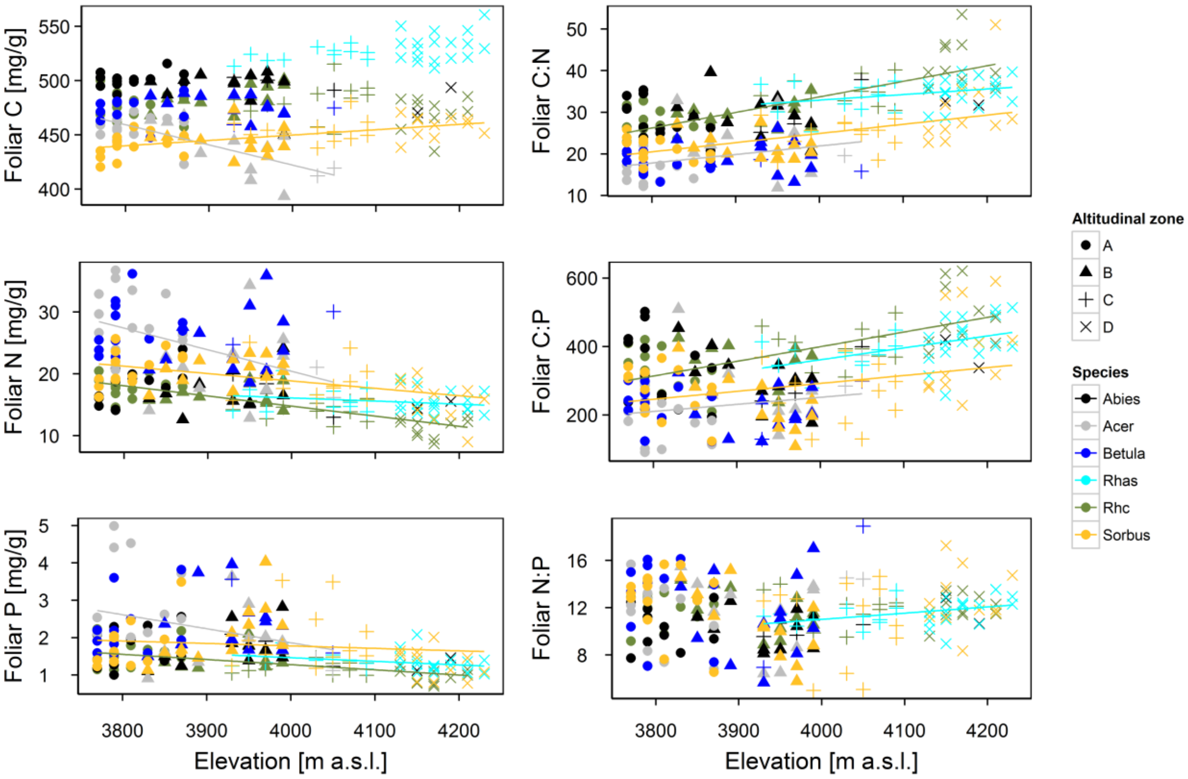

Figure 3. Changes in foliar C, N, and P concentrations [mg g^{-1}], and foliar C:N, C:P, and N:P ratios along the elevational gradient [m a.s.l.], and with regard to the different altitudinal zones A, B, C, D. Data originates from September 2015. Lines indicate significant linear regressions at $P < 0.05$. The graphs include the tree and shrub species *Abies spectabilis* (Abies), *Acer caudatum* (Acer), *Betula utilis* (Betula), *Rhododendron campanulatum* (Rhc), *Rhododendron anthopogon/setosum* (Rhas), and *Sorbus microphylla* (Sorbus). Three tree species only (Abies, Rhc, Sorbus) occur in all altitudinal zones (A, B, C, D).

Foliar N concentrations decreased significantly with elevation [m a.s.l.], except for *Abies*, and for *Betula* in September 2015 (Fig. 3). In *Rhc* (Table 3), a significant decrease of foliar N concentrations with elevation [m a.s.l.] was determined at all sampling dates (May 2013: r = -0.76; May 2014: -0.67; Sep 2014: -0.69; Sep 2015: -0.77). Referred to altitudinal zones, an abrupt significant decline in foliar N concentrations (*Rhc*) occurred in particular at the transitions from B to C (May 2013, 2014), and from C to D (Sep 2014, 2015; Table 3). For the other species, we found significant differences between ABC and D (*Abies*; Table S4), AB and CD (*Sorbus*; Table S5), AB and C (*Betula*; Table S7), and C and D (*Rhas*; Table S8). The deciduous species *Acer*, *Betula*, and *Sorbus* had significantly higher foliar N concentrations compared to the evergreen species *Abies*, *Rhc*, and *Rhas* (resulting from a one-way ANOVA).

Foliar P concentrations decreased significantly with elevation [m a.s.l.] in *Acer*, *Rhc*, and *Sorbus*, but not in *Abies*, *Betula*, and not in May 2014 and September 2014 in *Rhas*. The strongest significantly negative correlations with elevation [m a.s.l.] were detected in *Rhc* (May 2013: r = -0.50; May 2014: -0.62; Sep 2014: -0.43; Sep 2015: -0.62) (Fig. 3). A one-way ANOVA resulted in significant differences in *Abies* foliar P concentrations between the elevational zones ABC and D, and AB and CD (May 2014) (Table S4). In *Acer*, *Rhc*, and *Sorbus*, foliar P concentrations dropped from B to C, and most notably at the transition from C to D (Tables 3, S5, S6). In *Rhas*, foliar P concentrations were different between C and D in May 2013 and September 2015 (Table S8). The deciduous species had significantly higher foliar P concentrations than the evergreen species (one-way ANOVA).

We found significantly positive correlations between foliar C:N ratios and elevation [m a.s.l.] in *Rhc*, *Sorbus*, *Rhas* (May 2013, Sep 2015), *Betula* (Sep 2014), and *Acer* (Sep 2015) (Fig. 3). The most remarkable significant increase in foliar C:N ratios showed *Rhc* (May 2013: r = 0.77; May 2014: 0.71; Sep 2014: 0.65; Sep 2015: 0.79; Table 3) and *Sorbus* (Sep 2014: 0.71; Sep 2015: 0.50). Foliar C:N ratios differed significantly between the subalpine forest (zones AB), krummholz (C), and the alpine tundra (D) in *Rhc* (Table 3) and *Sorbus* (Table S5). In *Abies*, zone D varied significantly from zones ABC (Table S4). Foliar C:N ratios in *Acer* were significantly different between zones A and BC (Table S6).

Foliar C:P ratios increased significantly with elevation [m a.s.l.] in *Rhc*, *Sorbus*, *Rhas* (May 2013, Sep 2015), and *Acer* (Sep 2015) (Fig. 3). The increase was observed especially in *Rhc* (May 2013: 0.51; May 2014: 0.48; Sep 2014: 0.57; Sep 2015: 0.59). The stoichiometric ratios of C and P varied significantly between the subalpine forest (zones AB), and krummholz (C) and tundra (D), respectively, in *Rhc*, *Abies*, and *Sorbus* (Tables 3, S4, S5).

In contrast to C:N and C:P, the N:P ratios in each species were relatively constant with elevation [m a.s.l.], and usually did not change significantly between the altitudinal zones.

Table 3. Foliar C, N and P concentrations, and foliar C:N, C:P and N:P ratios in the species *Rhododendron campanulatum* in the altitudinal zones A (subalpine forest), B (uppermost subalpine forest), C (krummholz), and D (alpine tundra). Sampling took place in four field campaigns (May 2013, 2014; September 2014, 2015).

	Zone	**C [mg g^{-1}]**	**N [mg g^{-1}]**	**P [mg g^{-1}]**	**C:N**	**C:P**	**N:P**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
May 2013	A *(11)*	474.99 ± 5.49 ^{a}	15.62 ± 1.71 ^{a}	1.33 ± 0.27 ^{a}	30.71 ± 3.12 ^{a}	371.95 ± 77.05 ^{a}	12.07 ± 1.82 ^{a}
	B *(12)*	477.91 ± 4.96 ^{a}	15.09 ± 1.19 ^{a}	1.28 ± 0.27 ^{a}	31.85 ± 2.42 ^{a}	389.44 ± 76.53 ^{a}	12.13 ± 1.63 ^{a}
	C *(19)*	481.42 ± 5.40 ^{a}	12.66 ± 1.36 ^{b}	1.13 ± 0.23 ^{a}	38.46 ± 4.18 ^{b}	443.67 ± 87.73 ^{b}	11.64 ± 1.71 ^{a}
	D *(13)*	483.33 ± 16.35 ^{a}	11.13 ± 0.95 ^{c}	0.95 ± 0.13 ^{b}	43.69 ± 3.59 ^{c}	518.24 ± 83.49 ^{b}	11.91 ± 1.54 ^{a}
May 2014	A *(18)*	467.62 ± 12.38 ^{a}	16.19 ± 1.00 ^{a}	1.30 ± 0.12 ^{a}	28.98 ± 1.84 ^{a}	363.68 ± 34.09 ^{a}	12.56 ± 0.97 ^{a}
	B *(15)*	461.76 ± 16.20 ^{a}	15.70 ± 1.83 ^{a}	1.28 ± 0.23 ^{a}	29.79 ± 3.69 ^{a}	372.68 ± 77.58 ^{a}	12.48 ± 1.74 ^{a}
	C *(20)*	454.74 ± 26.30 ^{ab}	13.51 ± 1.89 ^{b}	1.08 ± 0.22 ^{b}	34.16 ± 4.12 ^{b}	433.49 ± 72.51 ^{b}	12.78 ± 2.11 ^{a}
	D *(12)*	470.76 ± 22.70 ^{ac}	12.24 ± 1.60 ^{b}	1.05 ± 0.15 ^{b}	38.81 ± 3.17 ^{c}	454.28 ± 50.91 ^{b}	11.70 ± 0.82 ^{a}
Sep 2014	A *(14)*	470.24 ± 15.69 ^{a}	20.30 ± 5.47 ^{a}	1.42 ± 0.26 ^{a}	24.72 ± 6.33 ^{a}	342.49 ± 65.65 ^{a}	14.74 ± 4.86 ^{a}
	B *(12)*	467.14 ± 25.71 ^{a}	19.58 ± 5.78 ^{a}	1.37 ± 0.20 ^{ab}	26.15 ± 8.57 ^{a}	351.06 ± 71.38 ^{a}	14.43 ± 4.00 ^{a}
	C *(12)*	467.80 ± 24.02 ^{a}	19.28 ± 4.70 ^{a}	1.33 ± 0.29 ^{ab}	25.93 ± 7.60 ^{a}	362.27 ± 57.92 ^{a}	15.03 ± 4.53 ^{a}
	D *(10)*	496.87 ± 45.51 ^{a}	14.40 ± 5.24 ^{b}	1.13 ± 0.14 ^{b}	36.90 ± 7.65 ^{b}	444.30 ± 56.61 ^{b}	12.87 ± 4.68 ^{a}
Sep 2015	A *(14)*	477.15 ± 11.25 ^{a}	18.05 ± 2.19 ^{a}	1.55 ± 0.34 ^{a}	26.81 ± 3.33 ^{a}	320.76 ± 67.47 ^{a}	11.87 ± 1.34 ^{a}
	B *(12)*	478.22 ± 26.02 ^{a}	18.16 ± 5.31 ^{a}	1.48 ± 0.33 ^{a}	27.84 ± 5.76 ^{a}	321.65 ± 96.80 ^{a}	11.33 ± 2.12 ^{a}
	C *(12)*	481.34 ± 16.75 ^{a}	14.19 ± 1.43 ^{a}	1.22 ± 0.17 ^{b}	34.21 ± 3.33 ^{b}	402.25 ± 54.53 ^{b}	11.78 ± 1.31 ^{a}
	D *(11)*	469.84 ± 14.73 ^{a}	11.44 ± 1.51 ^{b}	0.97 ± 0.19 ^{c}	41.70 ± 5.52 ^{c}	500.66 ± 91.46 ^{c}	11.96 ± 1.10 ^{a}

Values are means ± s.e.; different letters between two items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.*

Soil and foliar C:N:P relationships

Using bivariate linear regression analyses, we tested the relationships between topsoil C:N and foliar C:N ratios (Fig. 4) which were significant for *Rhc* (May 2013: $R^2 = 0.57$; May 2014: $R^2 = 0.48$; Sep 2014: $R^2 = 0.38$; Sep 2015: $R^2 = 0.56$). With respect to altitudinal zones, the linear regressions were significant in B (May 2013), C (May 2014, Sep 2014, 2015), and D (May 2014). Significant C:N relationships were also found for *Abies* (Sep 2014: $R^2 = 0.17$), *Sorbus* (Sep 2014: $R^2 = 0.18$), and *Acer* (Sep 2015: $R^2 = 0.12$).

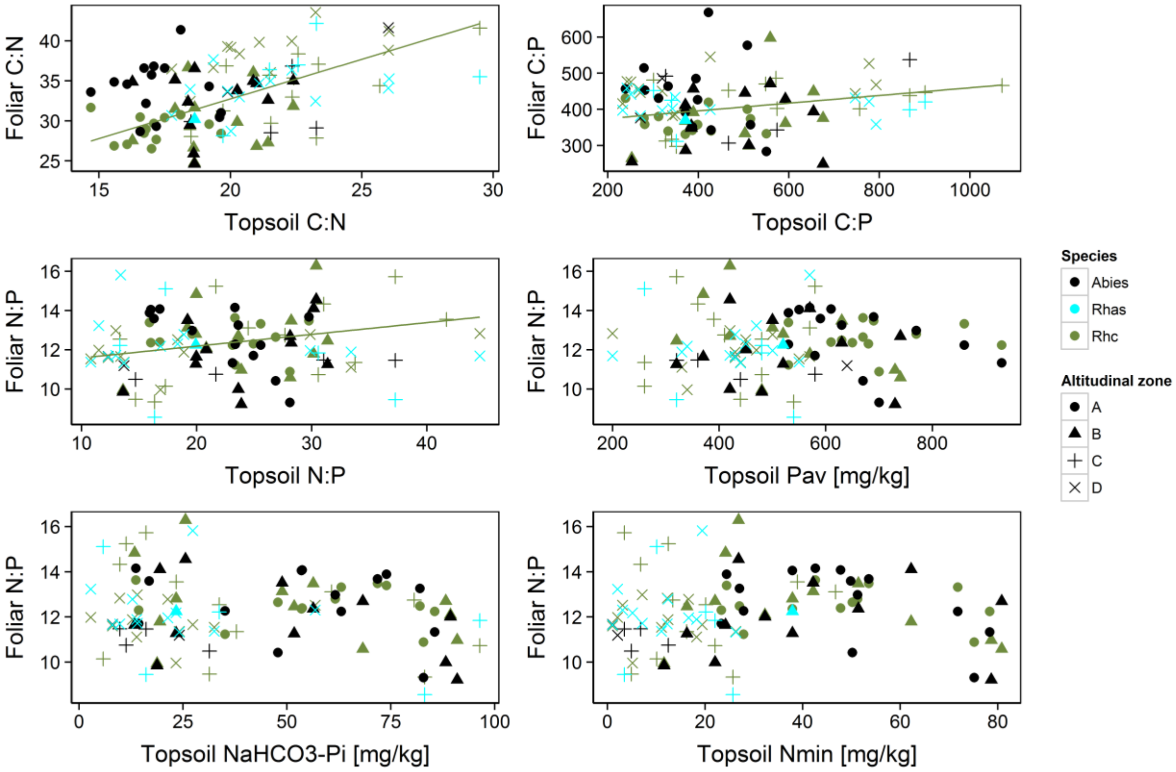

Figure 4. Relationships between topsoil C:N, C:P, N:P ratios and foliar C:N, C:P, N:P ratios, respectively, and topsoil P_{av}, $NaHCO_3$-P_i, N_{min} concentrations [mg kg^{-1}] and foliar N:P ratios for the species *Abies spectabilis* (Abies), *Rhododendron anthopogon/setosum* (Rhas) and *Rhododendron campanulatum* (Rhc). Data originates from May 2014. Lines indicate significant linear regressions at $P < 0.05$.

The same tests for C:P ratios resulted in a significant but weak relation for *Abies* (May 2013: $R^2 = 0.07$) and *Rhc* (May 2014: $R^2 = 0.18$; Fig. 4). *Rhc* showed a significant relation between foliar N:P and topsoil N:P ratios (May 2014: $R^2 = 0.14$; Fig. 4). We further tested linear regressions between topsoil P_{av} and foliar N:P ratios which were significant for *Rhas* in May 2013 only ($R^2 = 0.29$). The relationships between topsoil N_{min} and foliar N:P ratios were significant for *Abies* (0.13), *Rhas* (0.11), and *Acer* (0.20) in September 2015. We did not find significant relationships among topsoil $NaHCO_3$-P_i and foliar N:P ratios (Fig. 4). Multiple linear regression analyses used for testing the relations between foliar nutrients in each species individually, and soil nutrient availability and soil C:N:P stoichiometry revealed diverse results (Tables 4, S9). Foliar C:N and C:P ratios in *Rhc* were predominantly related to topsoil C:N ratios (Table 4). The other species showed more complex relationships, and especially for the deciduous tree species (e.g. *Betula*) the relations were often not significant.

Table 4. Multiple linear regression analyses for comparison of the relationships between foliar C:N:P stoichiometry in each species (*Rhc, Rhas, Abies, Acer, Betula, Sorbus*), and topsoil nutrient availability (N_{min}, P_{av}) and topsoil C:N:P stoichiometry.

	Foliar	***Rhc***	***Rhas***	***Abies***
May 2013	C:N	C:N***, N:P* (0.60, ***)	C***, C:N* (0.60, ***)	-
	C:P	N**, C:N* (0.34, ***)	-	C:P* (0.07, *)
	N:P	-	Pav** (0.29, **)	-
May 2014	C:N	C:N*** (0.48, ***)	Pav**, C:P**, Nmin** (0.52, **)	-
	C:P	C:N*, Nmin* (0.21, **)	-	-
	N:P	C:N*, C:P* (0.11, *)	N**, C*, C:N* (0.37, *)	C*, N*, C:P* (0.24, *)
Sep 2014 ^{2}	C:N	C:N*** (0.38, ***)	C:N* (0.13, *)	C:N**, C*, N* (0.22, *)
	C:P	C:N** (0.14, **)	N*, C* (0.24, *)	-
	N:P	C**, Nmin*, C:N* (0.13, *)	-	C**, N* (0.23, *)
Sep 2015 ^{2}	C:N	C:N***, C*** (0.72, ***)	-	-
	C:P	C:N***, C*** (0.48, ***)	-	Nmin* (0.14, *)
	N:P	-	Nmin* (0.11, *)	Nmin* (0.13, *)
		***Acer* ^{a}**	***Betula* ^{a}**	***Sorbus* ^{a}**
Sep 2014 ^{b}	C:N	-	-	C:N** (0.18, **)
	C:P	-	-	-
	N:P	-	-	-
Sep 2015 ^{b}	C:N	C:N* (0.12, *)	-	N*** (0.31, ***)
	C:P	Nmin* (0.18, *)	-	Nmin* (0.12, *)
	N:P	Nmin* (0.20, *)	C** (0.19, **)	-

Statistical significance at $P < 0.001$***, $P < 0.01$**, and $P < 0.05$* (multiple linear regression analyses). R^2 and *P* (as *, **, ***) of the linear models are shown *in parentheses.* “-“ means that no significant model was achieved. ^{a} In May 2013 and 2014, the deciduous tree species *Acer*, *Betula*, and *Sorbus* were not sampled (no leaves developed during field campaigns). ^{b} In September 2014 and 2015, Hedley soil P was not measured.

Discussion

Soil nutrient availability and C:N:P stoichiometry

Soil plant-available N_{min} and P_{av} concentrations as well as soil C:N:P ratios varied significantly with soil depth (Table S3), and were associated with an intense podzolization favored by precipitation sums of higher than 1000 mm a^{-1}, especially during the summer monsoon. This results in an outwash of soil organic matter (C in this case), and total and plant-available N and P concentrations from topsoils to subsoils (Fig. S1; Tables S1, S3). Podzolisation is a common process occurring from the upper montane belt to the treeline in the Himalaya (Bäumler, 2015). Apart from the organic layers Oi and Oe (Müller et al., 2016a), the highest mean soil C:N:P ratios occurred in topsoils. The fact, that soil nutrients declined considerably with soil depth, and that the investigated species are prevailing shallow-rooting trees, let us assume that the vertical transport of nutrients and potentially mineralizable SOM is a general problem in the study area impeding growing conditions for trees. Moreover, nutrient availability (esp. P) is generally limited by low soil pH (from 2.5 to 4), since under acidic conditions the availability of P commonly decreases due to precipitation of phosphate ions together with Al and Fe (Cross and Schlesinger, 1995; Khanna et al., 2007). We ascertained a high contribution of organic P fractions (biologically derived P_o) to total soil P concentrations (Table 1), which is a function of soil development in highly weathered soils (Cross and Schlesinger, 1995). Under such conditions, also P_o is fixed in metal-organic complexes.

Apart from explicit variations with soil depth, plant-available soil nutrient concentrations and soil C:N:P ratios differed with altitudinal variations in stand structures. According to that, our results suggest different nutrient dynamics in the alpine tundra (zone D) as compared to the subalpine forest (A), the uppermost subalpine forest (B), and krummholz (C). Wider topsoil C:N ratios with elevation suggest that decomposition of SOM decreases as a result of decreasing soil temperatures or soil moisture, and thus soil C concentrations increase, as we hypothesized above. Lower soil moisture availability in the alpine tundra (see Results) can decrease the accessibility of nutrients, hamper microbial growth, and consequently, induce N and P immobilization in microbial biomass and plants (Aponte et al., 2010). The wider C:N ratios in the alpine tundra, however, did not derive from the highest but the lowest topsoil C concentrations and even lower N concentrations. Moreover, the lowest topsoil C concentrations led to a significant decline of C:P and C:P_o ratios in the alpine tundra despite significantly lower P and P_o concentrations. This contradicts our first hypothesis that topsoil C concentrations would increase significantly with elevation solely due to hampered decomposition of SOM. Moreover, the lowest topsoil C concentrations in the alpine tundra are likely the result of a very low input of litter (thickness < 0.5 cm; see Results) from the dominant evergreen dwarf shrub species *Rhas* into soils. Nevertheless, in combination with a decrease in mineralization of a thin litter layer as it is suggested by closer relationships between soil C:N and litter C:N (Fig. 2), and soil C:P and litter C:P with elevation, this resulted in a low accumulation of SOM in alpine tundra soils. Additionally, a lower decomposition at higher elevations includes less mineralization of N and P, and thus lower soil N and P availability. Thus, we disprove our hypothesis that P availability is not affected by elevation. However, significantly closer topsoil N_{min}:P_{av} and N_{min}:NaHCO$_3$-P_i ratios with elevation (Table 2) are rather caused by a stronger decline in topsoil N availability than P availability. As stated in our first hypothesis, topsoil N:P_o ratios should remain constant since N and P_o are both governed by mineralization. However, again a stronger decrease in N relative to P_o in the alpine tundra (zone D) resulted in significantly lower N:P_o ratios in this area which is again likely caused by a very low litter input and less mineralization compared to the subalpine forest (AB) and krummholz (C). In krummholz (C), the highest topsoil C:P ratios and C concentrations occurred as compared to the subalpine forest (AB) and the alpine tundra (D). This derived likely from a well-developed litter layer (3-5 cm) caused by dense growing *Rhc* krummholz with a high input of litter, and thus input of OM into soils. However, litter accumulation and well-developed organic layers (Oe) suggest a decelerated decomposition of OM in this area, most likely as a consequence of the year-round lowest soil temperatures in this area.

Contrary to the results of Liptzin et al. (2012), we do not consider krummholz (zone C in our study) as an area of N and P accumulation. In their study, an accumulation of nutrients resulted from an interaction of krummholz vegetation with wind. In Rolwaling, topsoil N concentrations underneath krummholz (C) did not differ significantly from the subalpine forest (AB) below (Table 2). Moreover, soil N_{min} and P_{av} concentrations were significantly lower in zone C than in AB (Table 2) suggesting that other factors like hampered decomposition including N and P mineralization are responsible for the differences found. In line with our findings, they found the highest topsoil C concentrations underneath krummholz, however the differences in our study were not significant compared to the subalpine forest (AB) below. In Rolwaling, litter accumulation underneath dense growing *Rhc* krummholz led to relatively high topsoil C concentrations over time. In contrast to Liptzin et al. (2012), wider topsoil C:N and lower topsoil total and available N:P ratios in the alpine tundra compared to lower elevations (forest, krummholz) point to N limitation in this area. In the alpine tundra, N limitation of primary production was also found by Bowman et al. (1993) in Colorado who detected soil conditions favoring low mineralization rates of SOM in this area. Similar to our study, Huber et al. (2007) found decreasing soil total C, and soil total and plant-available N concentrations with elevation which they also interpreted to result from reduced rates of mineralization with elevation due to lower temperatures. Overall, comparing soil C:N:P stoichiometric patterns with other studies in alpine treeline ecotones is impeded by the fact that they are fully underrepresented in literature. Furthermore, a comparison with results from other studies not necessarily originating from alpine treelines is challenging, since the soil stoichiometry can vary among different study sites and spatial scales, and is among others affected by variations in abiotic environmental conditions, species composition, soil types, pedogenic processes, or plant ecological strategies (Zhao et al., 2014). As mentioned above, also varying determination methods of soil nutrients were used, and different fractions for C, N, and P were considered. The topsoil C:N:P ratios from this study (May 2013: 370:19:1; May 2014: 457:23:1) were twofold or more higher than a global scale mean of 186:13:1 (212:15:1 for forest soils; data mostly from topsoils, 0-10 cm) suggested by Cleveland and Liptzin (2007) who determined total C:N:P ratios. The remarkably higher C:N:P ratios in the study area may result from a generally hampered litter decomposition and low soil C turnover due to low temperatures, but also from the lower P_{av} compared to total P concentrations we used as soil component relevant for stoichiometric considerations.

Compared to Liptzin et al. (2012; data from 0-10 cm), who used total nutrient ratios, our results revealed lower topsoil C:N ratios underneath the subalpine forest (zones AB in our study), but higher topsoil C:N ratios in krummholz (C), and especially in the alpine tundra (D). Both, topsoil C:P and N:P ratios in our study were considerably higher (up to tenfold) which was due to distinctly higher C and N, respectively.

Summarizing, our results indicate lower decomposition rates at higher elevations leading to less mineralization of N and P, and thus lower soil N and P availability. Resulting from a stronger decline in total and available N compared to available P, the soil N:P, N_{min}:P_{av}, and N_{min}:$NaHCO_3$-P_i ratios decrease with elevation, pointing to N shortage in alpine tundra soils. We assume that the altitudinal changes in stand structures themselves govern nutrient cycling by the input of C, N, and P into soils by differences in litterfall.

Linking soil nutrient availability and C:N:P stoichiometry to foliar C:N:P stoichiometry

We hypothesized that the availability of soil nutrients controls tree growth limitation. Likewise to topsoil N, N_{min}, P, and P_{av} concentrations, the foliar N and P concentrations declined significantly with elevation [m a.s.l.], and with altitudinal changes in stand structures, especially at the transition from krummholz (C) to the alpine tundra (D; Tables 3, S4, S5, S8). Besides, a previous survey from Rolwaling (Müller et al., 2016a) revealed a significant decrease also in foliar potassium (K) and magnesium (Mg) concentrations with elevation [m a.s.l.], for what reason we assume a strengthened shortage in nutrients with elevation. These results contradict findings from various authors, who understood higher foliar N and P concentrations at high elevations as an adaptation to low temperature conditions that enhance metabolic activity and growth rates (e.g. Reich and Oleksyn, 2004; Han et al., 2005). Moreover, significantly decreasing foliar nutrient (N, P, K, Mg) concentrations with elevation in the majority of the investigated species in combination with significantly decreasing topsoil N, N_{min}, P, P_{av}, K, and Mg concentrations, let us assume that tree growth is rather source than sink limited, i.e. tree growth declines with elevation because the ability of trees to use available C is limited due to nutrient shortage and changing environmental conditions (e.g. drought stress, Müller et al., 2016a, b) as we hypothesized above. Since we determined exclusively foliar C concentrations, but not non-structural carbohydrates (NSC) like for example in Hoch and Körner (2003), Shi et al. (2008), and Sveinbjörnsson et al. (2010), interpretations regarding the C limitation hypothesis (Körner, 1998) were difficult. However, the lowest topsoil C, N, and P concentrations in the alpine tundra (D) and overall consistent foliar C concentrations with elevation let us assume that - apart from a strong limitation in N and P- growth conditions in the alpine tundra are affected by a C source rather than a C sink limitation. Moreover, significantly increasing foliar C:N and C:P ratios with elevation were caused by significantly decreasing foliar N and P and not by increasing C concentrations. Thus, trees may be unable to gain as much C or nutrients as they would be able to use for growth due to low nutrient availability or drought stress (Körner, 1998, 2012; Sveinbjörnsson et al., 2010).

According to that, significant relations between foliar C:N, C:P, and N:P ratios and topsoil stoichiometric ratios in *Rhc* (Fig. 4) suggest that this species likely depends on the nutrient source (stoichiometric plasticity). However, the variability in foliar C:P and N:P ratios explained was relatively small. In some species (e.g. *Abies, Acer, Rhas, Rhc*), the foliar N:P ratios -an indicator of nutrient limitation- were significantly related to topsoil N and P availability, at least at some sampling dates but with relatively low explained variances (Table 4). In contrast to our hypothesis above, equally decreasing foliar N and P with elevation led to relatively constant N:P ratios with elevation which may be caused by a co-limitation in N and P. Overall, foliar N and P concentrations were poor indicators of topsoil N and P availability as it was also found by Bowman et al. (2003) in the alpine tundra of the Colorado Rockies. They suggested that foliar nutrient concentrations might respond to variation in the ratios of supply of soil nutrients rather than variation in the supply of a single nutrient. In general, plants in low nutrient supply ecosystems like our study area were often shown to respond barely to soil nutrient availability as a consequence of adaptations which promote conservative use, loss, and uptake of nutrients (Bowman et al., 1993). This may explain the generally complex relationships between foliar stoichiometric ratios and soil nutrient availability we found. Especially for the deciduous tree species (e.g. *Betula*) the relations were often not significant (Table 4), and indicated foliar nutrient concentrations more independent of changing soil nutrient availability (stoichiometric homoeostasis) (cf. Sterner and Elser, 2002; Zhang et al., 2013; Sardans et al., 2015a). A main issue in the statistical analyses was that not all species occurred in each altitudinal zone (A, B, C, D). Due to that, especially *Rhc*, which was numerously existent in all zones, showed the statistically most reasonable results (Table 4). In contrast, species like *Acer* and *Betula* (A and B), and *Rhas* (C and D) were less frequent, and thus less data were available for analyzing soil-foliar nutrient relationships. Overall, our results cannot fully prove the ecological relevance of soil-foliar nutrient relationships in the study area.

Apart from that, foliar N:P ratios provided insights into potential nutrient limitation in Rolwaling. According to foliar N:P malnutrition thresholds, species in the study area were overall N limited (N:P < 14). Merely *Rhc* had slightly higher means in September 2014, however not in the alpine tundra (Table 3). According to Güsewell (2004), the tree and shrub species were found being co-limited by N and P in the study area (Tables 3, S4-S8). Other studies not originating from alpine treeline ecotones reported lower (e.g. Kang et al, 2011; Wu et al., 2012), similar (e.g. Sardans et al., 2015a), and higher foliar N:P ratios (e.g. Sterner and Elser, 2002; McGroddy et al., 2004; Han et al., 2005) compared to the study area. This is likely caused by species-specific variations in foliar N:P ratios limiting a direct comparison.

In summary, the results showed that tree species in the study area may interact differently with the nutrient availability in soils. We assume tree growth to be rather nutrient source than sink limited, most likely due to a shortage in N.

Conclusions

This paper leads to the following findings:

1. Soil nutrient availability and soil C:N:P ratios vary strongly with soil depth. Caused by high precipitation during the summer monsoon and coarse-grained soils with low water-holding capacities, the vertical transport of nutrients and potentially mineralizable SOM is a general problem in the study area impeding growing conditions for trees.

2. Soil N and P availability, and soil N:P and C:P ratios decrease, and soil C:N ratios increase significantly with elevation, especially at the transition from krummholz to the alpine tundra, indicating increasing nutrient shortage especially in this area. Nutrient availability (especially P) is generally limited by strongly acid soils.

3. The input of litter from vegetation and litter mineralization decrease with elevation, resulting in a low accumulation of SOM, and a low N and P availability in alpine tundra soils. Resulting from a stronger decline in total and available N compared to available P, the soil N:P, N_{min}:P_{av}, and N_{min}:$NaHCO_3$-P_i ratios decrease with elevation, pointing to N shortage in alpine tundra soils.

4. Contrary to previous studies, we do not consider the investigated alpine treeline ecotone as an area of nutrient accumulation. We assume that the altitudinal changes in stand structures themselves govern nutrient cycling by the input of C, N, and P into soils by differences in litterfall.

5. Tree species showed different relationships between foliar and soil stoichiometric ratios, and soil nutrient availability. We assume tree growth to be rather nutrient source than sink limited, most likely due to a shortage in N.

6. Significantly increasing foliar C:N and C:P ratios with elevation also suggest a limitation in N and P. Foliar N:P ratios point to N rather than P limitation.

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Supporting information

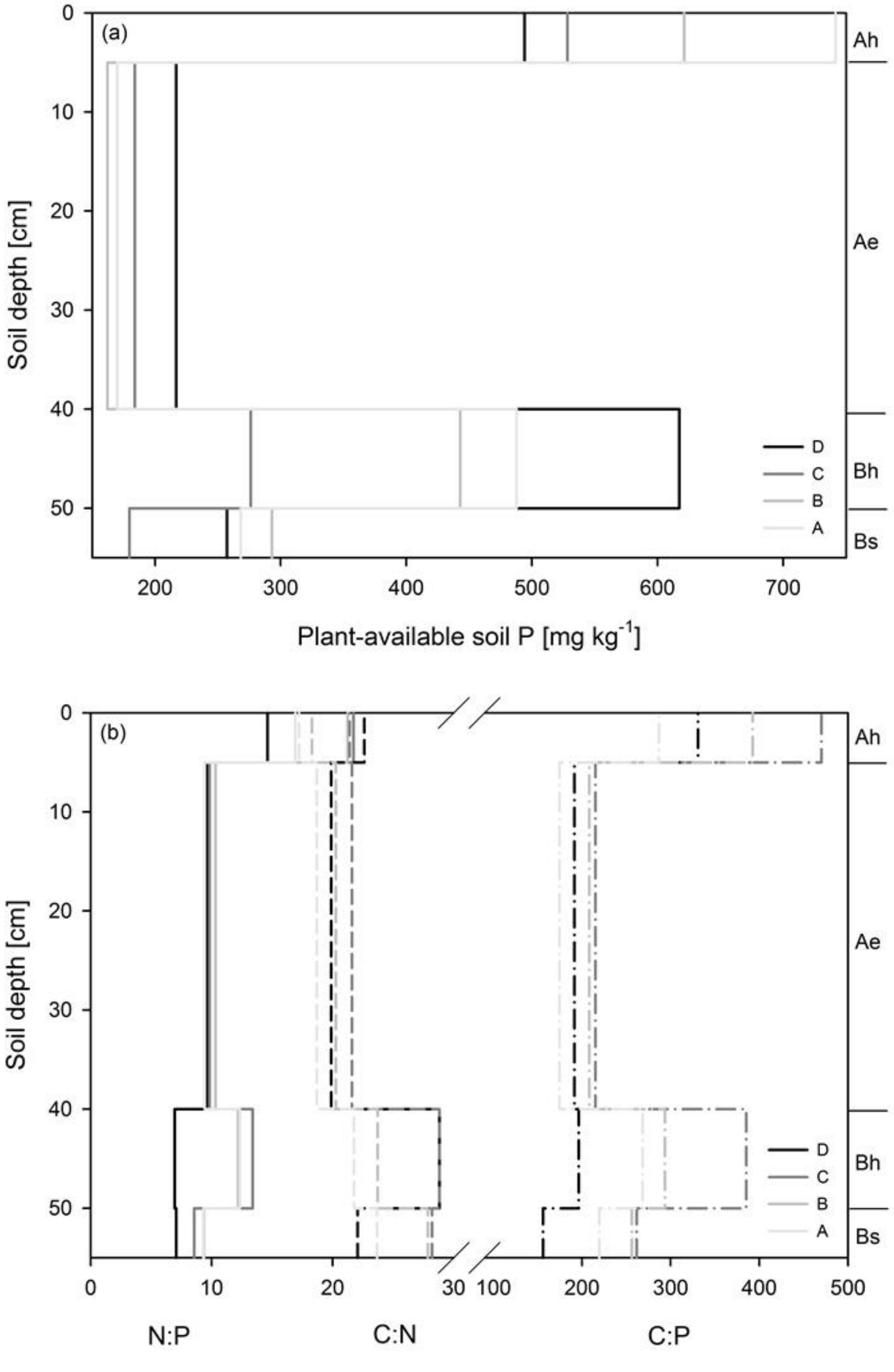

Figure S1. (a) Mean plant-available soil P_{av} (sum of Hedley-NaHCO$_3$, -NaOH fractions as soil components relevant for stoichiometric considerations), and (b) mean soil C:N, C:P, and N:P ratios with soil depth (Ah, Ae, Bh, Bs) in the different altitudinal zones A, B, C and D (data originates from May 2013). In order to improve the illustration of the results, we used standardized soil depths (0-5, 5-40, 40-50, 50+ cm) for the diverse soil horizons.

Table S1. Soil Nmin in the different soil horizons Ah, Ae, Bh, and Bs [mg kg^{-1}] of the different altitudinal zones A (subalpine forest), B (uppermost subalpine forest), C (krummholz), and D (alpine tundra). Sampling and on-site KCl extraction took place in three different field campaigns (May 2014; September 2014, 2015).

	Zone	**Nmin [Ah]**	**Nmin [Ae]**	**Nmin [Bh]**	**Nmin [Bs]**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
May 2014	A	44.70 ± 35.66 *(14)* ^{a}	2.09 ± 1.09 *(12)* ^{a}	5.58 ± 3.35 *(14)* ^{a}	1.95 ± 0.46 *(12)* ^{a}
	B	46.25 ± 37.89 *(12)* ^{a}	4.65 ± 2.71 *(12)* ^{a}	5.18 ± 1.32 *(4)* ^{ac}	2.34 ± 0.76 *(3)* ^{b}
	C	18.16 ± 13.70 *(12)* ^{b}	3.46 ± 3.22 *(11)* ^{a}	2.40 ± 1.64 *(3)* ^{b}	2.18 ± na *(1)* ^{b}
	D	12.17 ± 7.55 *(12)* ^{c}	4.59 ± 3.04 *(11)* ^{a}	2.88 ± 0.99 *(3)* ^{bc}	1.66 ± 0.56 *(6)* ^{b}
Sep 2014	A	21.54 ± 11.32 *(14)* ^{a}	4.35 ± 1.33 *(14)* ^{a}	6.07 ± 1.87 *(11)* ^{a}	5.25 ± 2.21 *(12)* ^{a}
	B	23.65 ± 12.11 *(12)* ^{a}	3.95 ± 1.58 *(12)* ^{a}	5.09 ± 1.22 *(6)* ^{ab}	4.21 ± 1.55 *(7)* ^{a}
	C	22.03 ± 9.72 *(12)* ^{a}	3.99 ± 1.68 *(10)* ^{a}	5.27 ± 2.23 *(4)* ^{b}	3.09 ± 0.08 *(2)* ^{b}
	D	10.40 ± 2.56 *(12)* ^{b}	4.31 ± 2.31 *(12)* ^{a}	5.08 ± 1.99 *(2)* ^{b}	2.92 ± 0.20 *(5)* ^{b}
Sep 2015	A	16.66 ± 13.13 *(14)* ^{a}	1.55 ± 0.55 *(14)* ^{a}	2.19 ± 0.97 *(13)* ^{a}	1.93 ± 1.25 *(14)* ^{a}
	B	13.26 ± 6.02 *(12)* ^{a}	2.02 ± 1.07 *(12)* ^{a}	2.66 ± 1.01 *(9)* ^{a}	1.96 ± 1.39 *(8)* ^{a}
	C	10.49 ± 2.63 *(12)* ^{b}	2.42 ± 2.23 *(12)* ^{a}	1.81 ± 0.66 *(7)* ^{b}	1.73 ± 0.44 *(3)* ^{b}
	D	7.39 ± 2.75 *(12)* ^{c}	2.04 ± 0.76 *(12)* ^{a}	1.84 ± 0.66 *(9)* ^{b}	1.40 ± 0.37 *(10)* ^{b}

Values are means ± standard error (s.e.); different letters between four items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA resp. Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.* Nmin = mineralised nitrogen (NH_4-N, NO_3-N); Ah, Ae, Bh, Bs = soil horizons.

Table S2. Topsoil C, N, P_{av}, P_o [mg g^{-1}], and N_{min} [mg kg^{-1}] concentrations, and topsoil C:N, C:P, C:P_o, N:P, N:P_o, N_{min}:P_{av}, and Nmin:$NaHCO_3$-P_i ratios in the different altitudinal zones A (subalpine forest), B (uppermost subalpine forest), C (krummholz), and D (alpine tundra). Sampling took place during four different field campaigns (May 2013, 2014; September 2014, 2015). Hedley-P was not measured in September 2014 and 2015.

	Zone	**C [mg g^{-1}]**	**N [mg g^{-1}]**	**Nmin [mg kg^{-1}]**	**Pav [mg g^{-1}] ***	**Po [mg g^{-1}] ***	**C:N**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
May 2013	A *(14)*	204.20 ± 84.82 ^{a}	12.11 ± 5.49 ^{a}	no data	0.74 ± 0.18 ^{a}	0.62 ± 0.17 ^{a}	17.22 ± 1.15 ^{a}
	B *(12)*	235.01 ± 67.79 ^{a}	12.98 ± 3.37 ^{a}	no data	0.62 ± 0.16 ^{a}	0.46 ± 0.15 ^{b}	18.27 ± 2.59 ^{b}
	C *(12)*	245.10 ± 73.91 ^{ab}	11.41 ± 3.25 ^{a}	no data	0.53 ± 0.10 ^{b}	0.41 ± 0.09 ^{b}	21.39 ± 1.59 ^{c}
	D *(10)*	171.02 ± 70.10 ^{ac}	7.39 ± 3.58 ^{b}	no data	0.49 ± 0.15 ^{b}	0.37 ± 0.10 ^{b}	22.59 ± 2.37 ^{c}
May 2014	A *(14)*	240.95 ± 96.67 ^{a}	13.99 ± 5.56 ^{a}	44.70 ± 35.66 ^{a}	0.61 ± 0.18 ^{a}	0.46 ± 0.14 ^{a}	17.26 ± 1.46 ^{a}
	B *(12)*	244.36 ± 101.80 ^{a}	12.44 ± 4.66 ^{a}	46.25 ± 37.89 ^{a}	0.54 ± 0.13 ^{a}	0.40 ± 0.11 ^{b}	19.40 ± 1.77 ^{a}
	C *(12)*	274.44 ± 107.70 ^{a}	12.05 ± 4.13 ^{ab}	18.16 ± 13.70 ^{b}	0.50 ± 0.20 ^{b}	0.39 ± 0.16 ^{b}	21.52 ± 2.91 ^{b}
	D *(12)*	180.92 ± 76.27 ^{b}	8.35 ± 2.81 ^{b}	12.17 ± 7.55 ^{c}	0.48 ± 0.10 ^{b}	0.43 ± 0.11 ^{b}	21.61 ± 2.63 ^{b}
Sep 2014	A *(14)*	244.02 ± 84.81 ^{a}	14.44 ± 5.01 ^{a}	21.54 ± 11.32 ^{a}	no data	no data	16.97 ± 1.41 ^{a}
	B *(12)*	295.80 ± 65.41 ^{a}	15.94 ± 3.53 ^{a}	23.65 ± 12.11 ^{a}	no data	no data	18.61 ± 1.29 ^{a}
	C *(12)*	300.20 ± 72.84 ^{a}	14.70 ± 3.42 ^{a}	22.03 ± 9.72 ^{a}	no data	no data	20.21 ± 1.31 ^{b}
	D *(12)*	136.66 ± 84.01 ^{b}	6.37 ± 3.46 ^{b}	10.40 ± 2.56 ^{b}	no data	no data	20.36 ± 3.94 ^{b}
Sep 2015	A *(14)*	311.26 ± 70.87 ^{a}	18.25 ± 4.30 ^{a}	16.66 ± 13.13 ^{a}	no data	no data	17.15 ± 1.35 ^{a}
	B *(12)*	332.26 ± 59.87 ^{a}	17.58 ± 2.77 ^{a}	13.26 ± 6.02 ^{a}	no data	no data	18.89 ± 1.54 ^{a}
	C *(12)*	323.26 ± 75.84 ^{a}	14.90 ± 3.25 ^{a}	10.49 ± 2.63 ^{b}	no data	no data	21.65 ± 2.09 ^{b}
	D *(12)*	235.44 ± 85.24 ^{b}	9.91 ± 2.74 ^{b}	7.39 ± 2.75 ^{c}	no data	no data	23.39 ± 2.57 ^{b}

Table S2. continued

	Zone	C:Pav *	C:Po *	N:Pav *	N:Po *	Nmin:Pav *	Nmin:NaHCO$_3$-Pi *
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
May 2013	A *(14)*	286.91 ± 68.47 ^{a}	353.53 ± 108.72 ^{a}	16.90 ± 4.33 ^{ab}	20.82 ± 6.60 ^{a}	no data	no data
	B *(12)*	392.55 ± 91.32 ^{ab}	541.97 ± 134.96 ^{ab}	21.24 ± 5.44 ^{a}	29.19 ± 7.09 ^{b}	no data	no data
	C *(12)*	470.24 ± 135.92 ^{b}	620.52 ± 208.42 ^{b}	21.71 ± 5.83 ^{a}	28.67 ± 9.08 ^{b}	no data	no data
	D *(10)*	330.96 ± 131.09 ^{ab}	437.93 ± 162.99 ^{a}	14.62 ± 5.58 ^{b}	19.28 ± 6.82 ^{c}	no data	no data
May 2014	A *(14)*	395.54 ± 92.21 ^{a}	520.86 ± 140.17 ^{a}	22.80 ± 4.59 ^{a}	30.02 ± 7.46 ^{a}	0.06 ± 0.04 ^{a}	0.95 ± 0.60 ^{a}
	B *(12)*	470.82 ± 131.31 ^{ab}	606.69 ± 147.13 ^{ab}	24.10 ± 5.57 ^{a}	31.23 ± 6.94 ^{a}	0.08 ± 0.04 ^{a}	1.17 ± 0.88 ^{a}
	C *(12)*	589.90 ± 256.08 ^{b}	753.25 ± 335.42 ^{b}	25.82 ± 9.35 ^{a}	32.88 ± 12.12 ^{a}	0.04 ± 0.03 ^{b}	0.66 ± 0.57 ^{b}
	D *(12)*	348.15 ± 172.26 ^{a}	427.93 ± 190.92 ^{a}	15.52 ± 5.90 ^{b}	19.13 ± 6.77 ^{b}	0.02 ± 0.01 ^{b}	0.55 ± 0.34 ^{b}
Sep 2014	A *(14)*	no data	no data	no data	no data	no data	no data
	B *(12)*	no data	no data	no data	no data	no data	no data
	C *(12)*	no data	no data	no data	no data	no data	no data
	D *(12)*	no data	no data	no data	no data	no data	no data
Sep 2015	A *(14)*	no data	no data	no data	no data	no data	no data
	B *(12)*	no data	no data	no data	no data	no data	no data
	C *(12)*	no data	no data	no data	no data	no data	no data
	D *(12)*	no data	no data	no data	no data	no data	no data

Values are means ± standard error (s.e.); different letters between four items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.* No data = no data available. *As soil component relevant for stoichiometric considerations, the sums of NaHCO$_3$- and NaOH-P-fractions (Pav), and of NaHCO$_3$- and NaOH-Po (Po), and NaHCO$_3$-Pi were used for P.

Table S3. Soil C, N and P concentrations [mg g^{-1}], and calculated soil C:N, C:P and N:P ratios with soil depth in the different field campaigns (May 2013, 2014; September 2014, 2015). Ah, Ae, Bh, Bs = soil horizons. Hedley-P was not measured in September 2014 and 2015.

	Soil horizon	**C [mg g^{-1}]**	**N [mg g^{-1}]**	**Pav [mg g^{-1}]***	**C:N**	**C:P**	**N:P**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
May 2013	Ah *(52)*	218 ± 73 ^{a}	11 ± 4 ^{a}	0.71 ± 0.19 ^{a}	19.6 ± 2.9 ^{a}	370 ± 124 ^{a}	18.9 ± 5.8 ^{a}
	Ae *(50)*	37 ± 24 ^{b}	1.8 ± 0.9 ^{b}	0.23 ± 0.12 ^{b}	20.1 ± 3.3 ^{a}	196 ± 55 ^{b}	9.8 ± 2.1 ^{b}
	Bh *(20)*	124 ± 24 ^{c}	5.4 ± 1.1 ^{c}	0.55 ± 0.11 ^{a}	23.4 ± 2.5 ^{a}	283 ± 75 ^{c}	11.9 ± 2.6 ^{b}
	Bs *(32)*	61 ± 24 ^{d}	2.4 ± 0.7 ^{b}	0.37 ± 0.09 ^{b}	25.0 ± 5.1 ^{a}	221 ± 74 ^{c}	8.7 ± 2.1 ^{b}
May 2014	Ah *(50)*	236 ± 100 ^{a}	12 ± 5 ^{a}	0.54 ± 0.16 ^{a}	20.0 ± 3.0 ^{a}	457 ± 194 ^{a}	22.5 ± 7.4 ^{a}
	Ae *(49)*	56 ± 53 ^{b}	2.7 ± 2.3 ^{b}	0.21 ± 0.10 ^{b}	19.5 ± 3.4 ^{a}	228 ± 111 ^{b}	11.5 ± 4.4 ^{b}
	Bh *(29)*	107 ± 49 ^{c}	4.8 ± 2.1 ^{c}	0.43 ± 0.17 ^{c}	22.5 ± 3.8 ^{a}	278 ± 120 ^{b}	11.9 ± 4.2 ^{b}
	Bs *(25)*	81 ± 74 ^{c}	3.4 ± 4.0 ^{c}	0.30 ± 0.10 ^{c}	24.7 ± 4.3 ^{a}	235 ± 116 ^{b}	9.0 ± 3.4 ^{b}
Sep 2014	Ah *(50)*	244 ± 99 ^{a}	13 ± 5 ^{a}	no data	19.1 ± 2.6 ^{a}	no data	no data
	Ae *(48)*	38 ± 34 ^{b}	2.0 ± 1.7 ^{b}	no data	18.6 ± 3.1 ^{a}	no data	no data
	Bh *(23)*	100 ± 37 ^{c}	4.7 ± 1.6 ^{c}	no data	20.9 ± 2.5 ^{a}	no data	no data
	Bs *(28)*	76 ± 34 ^{c}	3.2 ± 1.4 ^{c}	no data	23.7 ± 4.8 ^{a}	no data	no data
Sep 2015	Ah *(50)*	295 ± 89 ^{a}	15 ± 5 ^{a}	no data	20.2 ± 3.1 ^{a}	no data	no data
	Ae *(50)*	42 ± 57 ^{b}	2.1 ± 3.1 ^{b}	no data	19.1 ± 3.1 ^{a}	no data	no data
	Bh *(38)*	113 ± 46 ^{c}	4.8 ± 1.6 ^{c}	no data	23.4 ± 3.6 ^{a}	no data	no data
	Bs *(35)*	77 ± 49^{d}	3.0 ± 1.7 ^{c}	no data	24.8 ± 5.6 ^{a}	no data	no data

Values are means ± standard error (s.e.); different letters between four items in a row indicate significant statistical difference between soil horizons at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.* na = no data available. No data = no data available. *As soil component relevant for stoichiometric considerations, the sum of $NaHCO_3$- and NaOH-P-fractions were used for P.

Table S4. Foliar C, N and P concentrations, and calculated C:N, C:P and N:P ratios for evergreen species ***Abies spectabilis*** in the different altitudinal zones A, B, C, and D. Sampling took place during four different field campaigns (May 2013, 2014; September 2014, 2015).

	Zone	C [mg g^{-1}]	N [mg g^{-1}]	P [mg g^{-1}]	C:N	C:P	N:P
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
May 2013	A *(16)*	484.48 ± 9.39 ^{a}	14.10 ± 1.72 ^{a}	1.18 ± 0.30 ^{a}	34.75 ± 3.55 ^{a}	428.74 ± 85.52 ^{a}	12.25 ± 1.64 ^{a}
	B *(13)*	482.37 ± 6.54 ^{a}	13.60 ± 1.58 ^{a}	1.34 ± 0.43 ^{a}	35.89 ± 3.98 ^{a}	389.26 ± 104.04 ^{a}	10.80 ± 2.52 ^{a}
	C *(3)*	479.06 ± 4.36 ^{a}	13.90 ± 1.48 ^{a}	1.15 ± 0.11 ^{b}	34.71 ± 3.61 ^{a}	420.41 ± 40.89 ^{b}	12.21 ± 1.75 ^{a}
	D *(4)*	481.54 ± 7.33 ^{a}	12.56 ± 1.17 ^{b}	1.14 ± 0.16 ^{b}	38.58 ± 3.51 ^{b}	427.86 ± 60.67 ^{b}	11.11 ± 1.36 ^{a}
May 2014	A *(17)*	470.68 ± 10.61 ^{a}	14.14 ± 1.56 ^{a}	1.19 ± 0.31 ^{a}	33.65 ± 3.49 ^{a}	421.36 ± 105.91 ^{a}	12.40 ± 2.14 ^{a}
	B *(12)*	455.84 ± 21.69 ^{a}	14.28 ± 2.40 ^{a}	1.30 ± 0.33 ^{a}	32.50 ± 3.84 ^{a}	367.53 ± 80.10 ^{b}	11.31 ± 2.03 ^{a}
	C *(4)*	483.51 ± 14.34 ^{a}	15.04 ± 3.29 ^{a}	1.21 ± 0.30 ^{a}	33.59 ± 8.85 ^{a}	418.88 ± 111.37 ^{a}	12.77 ± 3.78 ^{a}
	D *(2)*	457.74 ± 19.34 ^{a}	12.26 ± 1.33 ^{b}	1.08 ± 0.15 ^{b}	37.64 ± 5.67 ^{b}	430.92 ± 78.56 ^{a}	11.42 ± 0.37 ^{a}
Sep 2014	A *(14)*	480.58 ± 30.57 ^{a}	21.11 ± 5.48 ^{a}	1.82 ± 0.49 ^{a}	24.28 ± 6.55 ^{a}	281.81 ± 78.88 ^{a}	11.76 ± 1.97 ^{a}
	B *(12)*	484.54 ± 28.82 ^{a}	19.77 ± 4.34 ^{a}	1.67 ± 0.36 ^{a}	25.83 ± 6.98 ^{a}	308.42 ± 92.06 ^{a}	12.08 ± 2.20 ^{a}
	C *(3)*	494.74 ± 34.74 ^{a}	20.50 ± 8.30 ^{a}	1.61 ± 0.53 ^{a}	27.51 ± 12.83 ^{a}	324.98 ± 85.38 ^{a}	13.21 ± 9.48 ^{a}
	D *(2)*	493.01 ± 50.92 ^{a}	11.43 ± 0.30 ^{b}	1.29 ± 0.39 ^{b}	43.09 ± 3.31 ^{b}	395.57 ± 80.78 ^{b}	9.28 ± 2.59 ^{b}
Sep 2015	A *(14)*	501.01 ± 6.55 ^{a}	17.77 ± 2.93 ^{a}	1.66 ± 0.52 ^{a}	28.90 ± 4.64 ^{a}	330.40 ± 103.78 ^{a}	11.25 ± 2.17 ^{a}
	B *(12)*	494.44 ± 15.81 ^{a}	17.37 ± 3.06 ^{a}	1.71 ± 0.51 ^{a}	29.21 ± 4.92 ^{a}	309.09 ± 77.39 ^{a}	10.55 ± 1.96 ^{a}
	C *(3)*	498.17 ± 6.13 ^{a}	17.11 ± 3.66 ^{a}	1.74 ± 0.45 ^{a}	30.08 ± 6.79 ^{a}	301.12 ± 85.93 ^{a}	9.93 ± 0.55 ^{ab}
	D *(2)*	482.03 ± 16.41 ^{a}	14.97 ± 0.83 ^{b}	1.29 ± 0.23 ^{b}	32.21 ± 0.68 ^{b}	378.93 ± 56.17 ^{b}	11.75 ± 1.50 ^{b}

Values are means ± standard error (s.e.); different letters between two items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.*

Table S5. Foliar C, N and P concentrations, and calculated C:N, C:P and N:P ratios for deciduous species ***Sorbus microphylla*** in the different altitudinal zones A, B, C, and D. Sampling took place during two different field campaigns (September 2014, 2015).

	Zone	**C [mg g^{-1}]**	**N [mg g^{-1}]**	**P [mg g^{-1}]**	**C:N**	**C:P**	**N:P**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
Sep 2014	A *(14)*	453.93 ± 27.83 ^{a}	22.66 ± 4.31 ^{a}	2.44 ± 0.88 ^{a}	20.87 ± 4.98 ^{a}	199.58 ± 93.78 ^{a}	9.67 ± 4.15 ^{a}
	B *(12)*	469.91 ± 36.24 ^{a}	21.15 ± 4.88 ^{a}	2.84 ± 0.87 ^{ab}	23.86 ± 7.98 ^{a}	182.92 ± 63.26 ^{a}	8.28 ± 3.80 ^{a}
	C *(12)*	494.53 ± 34.50 ^{b}	15.40 ± 2.64 ^{b}	1.92 ± 0.88 ^{b}	33.08 ± 6.48 ^{b}	290.61 ± 88.44 ^{b}	9.13 ± 3.33 ^{a}
	D *(6)*	511.38 ± 27.52 ^{b}	13.20 ± 2.30 ^{b}	1.88 ± 0.26 ^{b}	39.59 ± 6.03 ^{c}	276.62 ± 42.65 ^{b}	7.14 ± 1.55 ^{a}
Sep 2015	A *(14)*	439.71 ± 10.94 ^{a}	20.90 ± 2.74 ^{a}	1.75 ± 0.62 ^{a}	21.36 ± 2.69 ^{a}	273.09 ± 70.99 ^{a}	12.73 ± 2.70 ^{a}
	B *(12)*	444.58 ± 12.62 ^{a}	20.61 ± 2.23 ^{a}	2.78 ± 1.75 ^{b}	21.86 ± 2.98 ^{a}	212.30 ± 101.68 ^{a}	9.46 ± 3.95 ^{a}
	C *(12)*	453.92 ± 10.77 ^{b}	18.80 ± 3.10 ^{ab}	1.97 ± 0.81 ^{a}	24.68 ± 3.62 ^{b}	262.14 ± 87.41 ^{a}	10.77 ± 3.49 ^{a}
	D *(11)*	458.01 ± 9.75 ^{b}	15.91 ± 3.33 ^{b}	1.31 ± 0.41 ^{c}	30.27 ± 8.11 ^{c}	385.87 ± 127.49 ^{b}	12.71 ± 2.49 ^{a}

Values are means ± standard error (s.e.); different letters between two items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.*

Table S6. Foliar C, N and P concentrations, and calculated C:N, C:P and N:P ratios for deciduous species ***Acer caudatum*** in the different altitudinal zones A, B, and C. Sampling took place during two different field campaigns (September 2014, 2015).

	Zone	**C [mg g^{-1}]**	**N [mg g^{-1}]**	**P [mg g^{-1}]**	**C:N**	**C:P**	**N:P**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
Sep 2014	A *(12)*	458.23 ± 22.15 ^{a}	28.77 ± 5.27 ^{a}	2.56 ± 0.79 ^{a}	16.78 ± 5.39 ^{a}	192.34 ± 51.79 ^{a}	12.00 ± 3.40 ^{a}
	B *(4)*	476.93 ± 18.88 ^{a}	25.30 ± 4.40 ^{b}	2.30 ± 0.64 ^{a}	19.43 ± 4.53 ^{b}	220.25 ± 61.76 ^{a}	11.43 ± 2.74 ^{a}
Sep 2015	A *(14)*	457.15 ± 12.21 ^{a}	28.58 ± 5.09 ^{a}	2.78 ± 1.14 ^{a}	16.51 ± 3.18 ^{a}	188.84 ± 66.72 ^{a}	11.23 ± 2.76 ^{a}
	B *(10)*	437.82 ± 24.89 ^{a}	21.21 ± 6.21 ^{a}	1.98 ± 0.77 ^{a}	22.33 ± 6.71 ^{b}	254.42 ± 109.24 ^{a}	11.51 ± 3.23 ^{a}
	C *(2)*	415.83 ± 5.00 ^{b}	18.60 ± 3.46 ^{b}	1.29 ± 0.23 ^{b}	22.78 ± 4.51 ^{b}	329.39 ± 63.70 ^{b}	13.47 ± 0.07 ^{b}

Values are means ± standard error (s.e.); different letters between two items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.*

Table S7. Foliar C, N and P concentrations, and calculated C:N, C:P and N:P ratios for deciduous species ***Betula utilis*** in the different altitudinal zones A, B, and C. Sampling took place during two different field campaigns (September 2014, 2015).

	Zone	**C [mg g^{-1}]**	**N [mg g^{-1}]**	**P [mg g^{-1}]**	**C:N**	**C:P**	**N:P**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
Sep 2014	A *(13)*	474.40 ± 8.07 ^{a}	24.67 ± 7.02 ^{a}	2.20 ± 0.84 ^{a}	21.15 ± 7.46 ^{a}	239.47 ± 71.86 ^{a}	12.45 ± 4.49 ^{a}
	B *(12)*	478.97 ± 13.57 ^{a}	21.71 ± 7.70 ^{a}	2.53 ± 1.52 ^{a}	24.39 ± 7.42 ^{a}	237.32 ± 93.54 ^{a}	10.24 ± 4.13 ^{a}
	C *(2)*	482.79 ± 7.85 ^{a}	14.31 ± 0.27 ^{b}	2.69 ± 0.58 ^{a}	33.76 ± 1.20 ^{b}	183.28 ± 36.40 ^{a}	5.45 ± 1.27 ^{b}
Sep 2015	A *(13)*	465.88 ± 22.87 ^{a}	26.97 ± 4.26 ^{a}	2.41 ± 0.97 ^{a}	17.58 ± 2.24 ^{a}	218.09 ± 69.29 ^{a}	12.51 ± 3.85 ^{a}
	B *(12)*	477.91 ± 9.42 ^{a}	24.89 ± 5.12 ^{a}	2.45 ± 1.14 ^{a}	19.92 ± 3.89 ^{a}	233.50 ± 107.03 ^{a}	11.70 ± 4.30 ^{a}
	C *(2)*	467.02 ± 10.92 ^{a}	21.38 ± 3.79 ^{b}	2.56 ± 1.66 ^{a}	17.19 ± 1.89 ^{a}	228.62 ± 143.66 ^{a}	12.90 ± 6.87 ^{a}

Values are means ± standard error (s.e.); different letters between two items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.*

Table S8. Foliar C, N and P concentrations, and calculated C:N, C:P and N:P ratios for evergreen species ***Rhododendron anthopogon/setosum*** in the different altitudinal zones (B), C, and D. Sampling took place during four different field campaigns (May 2013, 2014; September 2014, 2015).

	Zone	**C [mg g^{-1}]**	**N [mg g^{-1}]**	**P [mg g^{-1}]**	**C:N**	**C:P**	**N:P**
		Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.	Mean ± s.e.
May 2013	C *(7)*	503.84 ± 12.13 ^{a}	16.08 ± 1.44 ^{a}	1.41 ± 0.28 ^{a}	31.55 ± 2.94 ^{a}	375.52 ± 89.38 ^{a}	11.88 ± 2.24 ^{a}
	D *(15)*	510.79 ± 13.57 ^{a}	14.64 ± 0.99 ^{b}	1.23 ± 0.10 ^{b}	35.01 ± 2.11 ^{b}	416.64 ± 30.44 ^{a}	11.93 ± 0.95 ^{a}
May 2014	B *(1)*	514.55 ± na ^{a}	17.03 ± na ^{a}	1.39 ± na ^{a}	30.21 ± na ^{a}	371.47 ± na ^{a}	12.30 ± na ^{a}
	C *(7)*	514.03 ± 7.35 ^{a}	14.47 ± 1.89 ^{b}	1.28 ± 0.23 ^{b}	36.01 ± 4.28 ^{b}	411.10 ± 62.12 ^{b}	11.05 ± 1.76 ^{a}
	D *(22)*	520.51 ± 15.86 ^{a}	13.54 ± 1.66 ^{b}	1.26 ± 0.16 ^{b}	33.78 ± 2.85 ^{b}	418.81 ± 47.75 ^{b}	12.45 ± 1.67 ^{a}
Sep 2014	B *(2)*	514.13 ± 3.77 ^{a}	14.97 ± 4.56 ^{a}	1.19 ± 0.40 ^{a}	36.06 ± 11.24 ^{a}	460.87 ± 159.37 ^{a}	12.71 ± 0.46 ^{a}
	C *(11)*	498.13 ± 26.35 ^{a}	15.40 ± 5.02 ^{a}	1.19 ± 0.16 ^{a}	34.39 ± 7.06 ^{a}	424.08 ± 55.22 ^{a}	12.94 ± 3.44 ^{a}
	D *(23)*	503.66 ± 36.12 ^{a}	14.85 ± 3.82 ^{b}	1.14 ± 0.17 ^{a}	33.38 ± 7.21 ^{a}	448.85 ± 79.54 ^{a}	13.24 ± 4.12 ^{a}
Sep 2015	C *(11)*	524.09 ± 6.17 ^{a}	15.98 ± 2.10 ^{a}	1.42 ± 0.19 ^{a}	33.27 ± 3.97 ^{a}	375.54 ± 44.29 ^{a}	11.32 ± 0.93 ^{a}
	D *(18)*	531.58 ± 13.06 ^{a}	14.23 ± 1.77 ^{b}	1.31 ± 0.27 ^{b}	35.27 ± 3.31 ^{a}	419.43 ± 67.43 ^{b}	11.84 ± 1.18 ^{a}

Values are means ± standard error (s.e.); different letters between two items in a row indicate significant statistical difference between altitudinal zones at $P < 0.05$ (one-way ANOVA or Kruskal-Wallis test + Post hoc Tukey test). Number of observations is shown *in parentheses.*

Table S9. Multiple linear regression analyses. Seasonal comparison of the relationships between foliar C:N:P stoichiometry of the different species (*Rhc*, *Rhas*, *Abies*, *Acer*, *Betula*, *Sorbus*), and topsoil nutrient availability (Nmin, Pav) and C:N:P stoichiometry.

	Foliar	***Rhc***	***Rhas***	***Abies***	***Acer*** [1]	***Betula*** [1]	***Sorbus*** [1]
May 2013	C	N**, C*, Pav* (0.10, *)	-	-	no data	no data	no data
	N	C:N*** (0.54, ***)	N*** (0.66, ***)	-	no data	no data	no data
	P	N*** (0.27, ***)	C* (0.24, *)	Pav* (0.14, *)	no data	no data	no data
	C:N	C:N***, N:P* (0.60, ***)	C***, C:N* (0.60, ***)	-	no data	no data	no data
	C:P	N**, C:N* (0.34, ***)	-	C:P* (0.07, *)	no data	no data	no data
	N:P	-	-	-	no data	no data	no data
May 2014	C	N** (0.12, **)	-	-	no data	no data	no data
	N	C:N*** (0.41, ***)	Pav*, C:P*, N:P*, C* (0.37, *)	-	no data	no data	no data
	P	C:N** (0.17, **)	C:P*, N*, N:P*, C:N* (0.34, *)	-	no data	no data	no data
	C:N	C:N*** (0.48, ***)	Pav**, C:P**, Nmin** (0.52, **)	-	no data	no data	no data
	C:P	C:N*, Nmin* (0.21, **)	-	-	no data	no data	no data
	N:P	C:N*, C:P* (0.11, *)	Pav*, C*, C:N* (0.37, *)	C*, N*, C:P* (0.24, *)	no data	no data	no data
Sep 2014 [2]	C	C*** (0.24, ***)	-	-	-	-	C:N* (0.07, *)
	N	C:N*** (0.44, ***)	-	-	-	C*, N* (0.15, *)	C:N** (0.19, **)
	P	C:N*, Nmin*, N* (0.24, **)	N*, C* (0.22, *)	-	-	-	N**, C* (0.17, *)
	C:N	C:N*** (0.38, ***)	C:N* (0.13, *)	C:N**, C*, N* (0.22, *)	-	-	C:N** (0.18, **)
	C:P	C:N** (0.14, **)	N*, C* (0.24, *)	-	-	-	-
	N:P	C**, Nmin*, C:N* (0.13, *)	-	C**, N* (0.23, *)	-	-	-
Sep 2015 [2]	C	C* (0.09, *)	-	C:N* (0.18, *)	C:N** (0.22, **)	Nmin*** (0.51, ***)	N***, C** (0.22, **)
	N	C***, C:N*** (0.70, ***)	-	C:N*, N*, Nmin*, C* (0.24, *)	C*, N*, Nmin* (0.24, *)	N* (0.09, *)	N*** (0.30, ***)
	P	C:N***, C*** (0.44, ***)	-	Nmin* (0.14, *)	Nmin*, N*, C* (0.44, **)	-	-
	C:N	C:N***, C*** (0.72, ***)	-	-	C:N* (0.12, *)	-	N*** (0.31, ***)
	C:P	C:N***, C*** (0.48, ***)	-	Nmin* (0.14, *)	Nmin* (0.18, *)	-	Nmin* (0.12, *)
	N:P	-	Nmin* (0.11, *)	Nmin* (0.13, *)	Nmin* (0.20, *)	C** (0.19, **)	-

Statistical significance at $P < 0.001$***, $P < 0.01$**, and $P < 0.05$* (multiple linear regression analyses). R^2 and *P* (as *, **, ***) of the linear models are shown *in parentheses*. "-" means that no significant model was achieved. No data = no data available. [a] In May 2013 and 2014, the deciduous tree species *Acer*, *Betula*, and *Sorbus* were not sampled (no leaves developed during field campaigns).[b] In September 2014 and 2015, Hedley soil P was not measured.

Manuscript 4 (under review)

Nutrient deficiency in soils and trees of a treeline ecotone in Rolwaling Himal, Nepal

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Keywords: *Abies spectabilis*, foliar nutrients, Himalaya, nitrogen, nutrient cycling, nutrient limitation, podzol, *Rhododendron campanulatum*, soil nutrients, treeline.

Abstract

Background: At a global scale, tree growth in alpine treeline ecotones is limited by low temperatures. At a local scale, however, tree growth at its upper limit depends on multiple interactions of influencing factors and mechanisms.

Aims: The aim of our research is to understand local scale effects of soil properties and nutrient cycling on tree growth limitation, and their interactions with other abiotic and biotic factors in a near-natural Himalayan treeline ecotone.

Methods: Soil samples of different soil horizons, litter, decomposition layers, and foliage samples of standing biomass were collected in four altitudinal zones along three slopes, and were analysed for exchangeable cations and nutrient concentrations, respectively. Additionally, datasets on soil temperature, soil surface temperature, soil moisture, air temperature, precipitation, and tree physiognomy patterns were evaluated.

Results: Both soil nutrients and foliar macronutrient concentrations of nitrogen (N), magnesium (Mg), potassium (K), and partially phosphorus (P) decrease significantly with elevation. Foliar manganese (Mn), by contrast, is extraordinarily high at high elevation sites. Potential constraining factors on tree growth were identified using multivariate statistical approaches.

Conclusions: We assume tree growth, treeline position and vegetation composition being strongly affected by nutrient limitation, which in turn, is governed by low soil temperatures and influenced by soil moisture conditions.

Introduction

From a global perspective, tree growth in natural alpine treeline ecotones is limited by low temperatures (e.g., Tranquillini 1979; Jobbágy and Jackson 2000; Körner and Paulsen 2004). At a local scale, however, tree growth at its upper limit depends on multiple interactions of influencing factors and mechanisms, which are extensively reviewed in Holtmeier (2009) and Körner (2012). Previous studies give evidence of treelines to be both, nutrient sinks (e.g., Körner 1989, 2012; Saxe et al. 2001; Hoch et al. 2002; Hoch and Körner 2003; Shrestha et al. 2007; Liptzin et al. 2012; Fajardo et al. 2013) and nutrient depletion areas (e.g., Sveinbjörnsson 2000; Richardson et al. 2004; Loomis et al. 2006; Huber et al. 2007; McNown and Sullivan 2013; Shi and Wu 2013). Most studies on nutrient cycling in treeline ecotones focus on carbon (C), nitrogen (N), or phosphorus (P) foliar concentrations of trees in alpine treeline ecotones (e.g., Körner 1989; Garkoti and Singh 1994; Gieger and Leuschner 2004), whereas only a few studies address soil nutrient concentrations and availability (focus on N, P) (e.g., Loomis et al. 2006; Huber et al. 2007; Liptzin et al. 2012). N is considered as the most limiting nutrient to primary production in terrestrial plants, and thus also in treeline trees (Haselwandter 2007; Huber et al. 2007). Besides, P availability is considered to limit plant growth, since P is essential for the energy metabolism in plants (Haselwandter 2007; Fageria and Moreira 2011). However, only little is known about the function of nutrient cycling in treeline ecotones and the effect of soil properties, such as soil nutrients, soil temperature, and soil moisture on tree growth in high altitude environments, especially with regard to soil nutrient availability, and nutrient uptake and investment by treeline trees (Müller et al. 2016).

The aim of this study is to understand local scale effects of soil properties and nutrient cycling on tree growth limitation and their interactions with other abiotic and biotic factors in a near-natural treeline ecotone of Rolwaling Himal, Nepal. We assessed soil pedogenic processes, and soil, litter, and foliar nutrient concentrations of C, N, P, K, Mg, Ca, Mn, Fe, and Al along three altitudinal transects. Further, multiple regression analyses (MLR) were implemented to identify the factors best suited for the description of changes in elevation, and to reveal interactions of nutrient concentrations, soil properties, tree physiognomy patterns, and climatic variables.

Materials and methods

Study area

The study area is located in the Rolwaling Himal in the northeastern part of Central Nepal, south of the village Beding (N 27°54', E 86°22'; Fig. 1). It is part of the southern declivity of the Himalaya Mountains and belongs to the Gaurishankar Conservation Area. Climate in the study area (cf. Gerlitz et al. 2015) is warm temperate with cold dry winters and cool wet summers (Cwc-climate, Kottek et al. 2006) characterised by heavy monsoon rains. Parent material is pegmatitic rock of granitic composition. Topography exhibit generally steep slopes with a mean inclination of 37°. Creeks and gullies frequently cut deep into slopes. Soil depth varies from 30 to 70 cm, with maximum skeletal fractions from 75 to 95 % in Ae horizons. Broad sections of the Rolwaling treeline ecotone are near-natural due to its geographic isolation and low population density, thus human impact is negligible (Schickhoff et al. 2015).

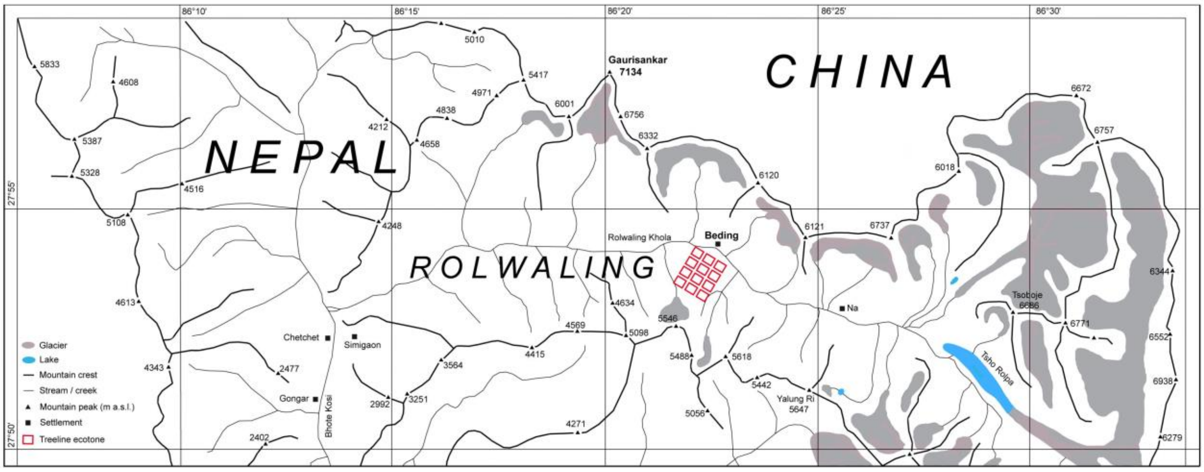

Fig. 1. Study area (adapted from König 2003).

The treeline ecotone is characterised by a gradual decrease of tree height and tree population density with elevation. In lower elevation, a comparatively dense forest cover occurs. Vegetation composition here is dominated by tree species *Betula utilis* and *Abies spectabilis*. Other tree species such as *Acer caudatum*, *Rhododendron campanulatum* and *Sorbus microphylla* occur less frequently. A krummholz belt, dominated by almost impenetrable

Rhododendron campanulatum thickets follows beyond closed forests, where scattered small individuals of *Sorbus microphylla* intersperse. *Acer caudatum* is absent here, while *Abies spectabilis* and *Betula utilis* occur rarely, and mostly as small patches of individuals. The alpine tundra above the krummholz zone is treeless and characterised by a mosaic pattern of dominating dwarf shrub species *Rhododendron anthopogon* and *Rhododendron setosum*. Some saplings of *Rhododendron campanulatum* and *Betula utilis*, as well as *Sorbus microphylla* and a few crippled *Abies spectabilis* individuals appear.

Sampling design and field data collection

Soil, litter, and foliage sampling was conducted in April and May 2013 and 2014, respectively, collection of additionally in August and September 2013 and 2014. We chose a stratified random sampling design with a preselection of three slopes, two northeast-exposed slopes (NE1, NE2), one northwest-exposed slope (NW1), divided into four altitude-dependent zones A, B, C, and D (Fig. 2a). Classification into zones was based on the distribution of arborescent vegetation. Within each zone of each slope, four different experimental plots (20 m x 20 m) were randomly selected (Fig. 2a). In total, we sampled 48 plots (3 slopes x 4 altitudinal zones x 4 plots). On the NE slopes, altitudinal zone A ranges from 3780 to 3900 m a.s.l. (closed forest), followed by zone B (3920 - 3990 m a.s.l.; uppermost closed forest), zone C (4010 m - 4100 m a.s.l.; krummholz), and zone D (4120 m - 4250 m a.s.l.; alpine tundra). On the NW1 slope, zones are located about 100 meters lower in altitude (Fig. 2a).

From three soil profiles per plot (Fig. 2b), horizon-wise samples were combined to composite samples. Samples of litter (L) and decomposition layers (Of) were collected using a sampling frame (20 cm x 20 cm). Moreover, needles and leaves of standing biomass (SB), i.e. of living evergreen trees of *Abies spectabilis* and *Rhododendron campanulatum*, were sampled adjacent to soil profiles. A total of 310 soil samples, 294 L samples, 271 Of samples, and 249 SB samples could be acquired in 2013 and 2014.

Botanical nomenclature refers to Press et al. (2000). DBH of all tree species individuals were measured with a diameter measuring tape at 1.3 m above ground level. Tree individuals with DBH ≥ 7 cm were identified and counted on each plot. Heights and crown diameters of all trees with DBH ≥ 7 cm were measured using a laser dendrometer (Laser Technology Criterion RD 1000, MDL Laser Ace 300). Further, we installed 34 modified *WiFi* sensors (Koubachi Inc.), which have been monitoring hourly soil temperature (ST) and soil moisture (pF) at 10 cm depth, respectively, and soil surface air temperature (AT). Three automatic meteorological stations (HOBO U30-NRC, Onset Computer Corporation) have been measuring air temperature and precipitation in a temporal resolution of 15 minutes (cf. Gerlitz et al. 2016).

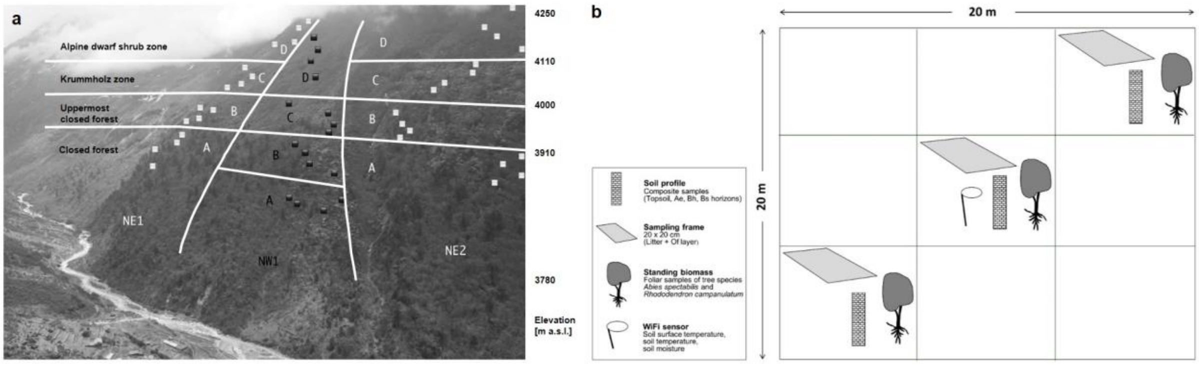

Fig. 2. Sampling design. **a.** Slope transects (NE1, NW1, NE2) are divided into four altitudinal zones (A, B, C, D), each represented by four randomly selected 20 m x 20 m experimental plots. **b.** Sampling design of the respective plots.

Laboratory analyses

Total C and total N of all samples were determined using *elemental analyzer vario EL III*. Effective cation exchange capacity (CEC) of soils and Of was analysed using inductively coupled plasma optical emission spectrometry (*ICP-OES)*, L and SB samples were dissolved by microwave-digestion beforehand (*MLS START 1500 Microwave Extractor*; 4 ml HNO_3, 3 ml H_2O_2, 5 ml H_2O). pH values of soils and Of were detected electrometrically in 1 M KCl and in distilled H_2O at a ratio of 1:2.5 (*WTW ProfiLine pH 3310*). Humus quality was determined by potential cation exchange capacity (CECpot) and C/N ratios, respectively. CECpot was calculated by dividing values of CEC by a pH-dependent factor of 0.15 (Ad-hoc AG Boden 2005).

Statistical analyses

Statistical analyses were implemented with the programming language R (version 3.1.2, R Foundation for Statistical Computing, Vienna, AT), graphs were created with R and Sigmaplot (version 10.0, Systat Software Inc., San Jose, US). For the implementation of MLR, elevation of sampling sites serves as dependent variable and overall 27 independent variables: AT, ST, pF. CEC, exchangeable cations Na^+, K^+, Mg^{2+}, Ca^{2+}, Mn^{2+}, Al^{3+}, H^+, total N, C, S, P, C/N ratio, slope inclination (SL), base saturation, anion exchange capacity, humus content, altitudinal levels and plot-wise means of vegetation-related parameters DBH, tree height, crown diameter hillside, crown diameter parallel, and number of tree individuals. Multicollinearity between independent variables was set $R^2 \geq 0.80$. MLR were performed for decomposition layer and topsoil horizon results in 2013 and 2014, respectively.

Results

Climate data

Based on the average of three climate stations (April 2013 to April 2014), we measured a mean air temperature of 3.3 ± 0.5°C, a mean minimum temperature of -12 ± 0.3°C and a mean maximum temperature of 17.3 ± 0.6°C. The seasonal variability of air temperatures is in line with the soil temperatures measured at plot level.

Soil temperature data reveal a mean of 3.2 ± 0.7°C in 10 cm soil depth for the period from 1st of May 2013 to 30th of April 2014. For the growing season (end of April to end of October 2013), we measured a mean of 7.8 ± 0.6°C. At the treeline formed by *Abies spectabilis* and *Betula utilis* (transition from B to C), we detected a growing season mean soil temperature of 7.6 ± 0.6°C. Soil temperatures show a general negative altitudinal gradient regardless of vegetation cover. Average annual precipitation is 1298 ± 61 mm. Monsoon rainfall appears from June to October with an accumulated precipitation of 1125 ± 44 mm in 2013 (87 % of annual precipitation). This is reflected by soil moisture data featuring lowest pF values (0.94 ± 0.19) during monsoon in August 2013 and highest in January 2014 (4.72 ± 0.32).

General pedogenic processes and features

The main pedogenic process is leaching of dissolved organic carbon, Al, and Fe from topsoil to subsoil. Accordingly, soil types in the study area were classified as podzols (IUSS 2006). Due to their colour, texture (mainly sand), total C, and cation exchange capacities, mineral horizons were differentiated in topsoils (Ah), bleached horizons (Ae), and illuviation horizons (black Bh, reddish-brown Bs) enriched in soil organic matter and sesquioxides. The ash-grey eluviation horizons (Ae) are very poor in Al, Fe, and C. The latter are predominantly accumulated in black illuviation horizons (Bh) demonstrating the lowest mean base saturation compared to the other horizons. Soil analyses reveal acid pH values (KCl) from 2.64 to 4.27, increasing with soil depth (Appendix A). pH measured in KCl solution is on average 0.95 units lower than in distilled H_2O. Besides, K, Mg and Ca are accumulated in the subsoil, predominantly in Bh. CEC is also higher in Bh compared to Ae, however, base saturation in Bh is the lowest of all horizons.

Total carbon, C/N ratio, humus quality

Total C varies considerably between different sample materials (SB, L, Of, mineral soil horizons). Means decline from SB to L, Of, topsoils, and Ae, increase in Bh, and drop again in Bs (Appendix A). Mean of soil organic matter in topsoils is 372.8 mg g^{-1} (2014: 388.4 mg g^{-1}), and is highest in Of with 840.6 mg g^{-1} (2014: 725.6 mg g^{-1}). Total litter C and total Of C do not show any significant altitudinal trend but rather remains stable. However, in topsoils and Ae horizons we found slightly increasing total C from zone A to C, and a sharp decline in zone D. C/N ratios decrease from L to Of, to topsoils and Ae, and increase again in Bh and Bs (Appendix A). We detected a highly significant relationship between elevation (m a.s.l.) and topsoils ($r = 0.75$), Of layers ($r = 0.73$), and L ($r = 0.60$). Results from 2014 (Of: $r = 0.68$; topsoils: $r = 0.57$; L: $r = 0.43$) are slightly lower. Minimum CECpot for topsoils is 36.12 cmol kg^{-1}, maximum is 257.90 cmol kg^{-1}, and mean is 105.50 cmol kg^{-1}. Based on these results, we classified humus quality of 43 samples (84.34 %) as very low (Ad-hoc AG Boden 2005). Similarly, 94 % of C/N values in the range from 15 to 25 indicate a medium to low humus quality. Humus form was classified as mor-like moder. These results were confirmed in 2014.

Total nitrogen

Just as total C, total N differs widely between different sample materials (Appendix S1). Total N proportions were highest in Of, followed by SB. Topsoils show similar values as L. Total N strongly decreases with soil depth, showing lowest concentrations in Ae and Bs, however an accumulation of N in Bh. Total N in SB (cf. foliar nutrients), L, Of, topsoils, Bh and Bs horizons decreases with elevation (m a.s.l.). Results from 2013 indicate the strongest negative correlations between elevation and total Of N (black; r = -0.81, 2014: r = -0.75), and total litter N (grey; r = -0.67, 2014: r= -0.44), respectively (Fig. 3).

For total litter N and Of N, we detected great differences between the closed forest (A, B), and krummholz and alpine tundra (C, D) (Fig. 4). A similar distribution was observed for Bs horizons with a mean of 2.67 mg g^{-1} (2014: 2.92 mg g^{-1}) under closed forest, 1.96 mg g^{-1} (2.2 mg g^{-1}) under krummholz (C), and 1.66 mg g-1 (1.78 mg g^{-1}) under alpine tundra (D). A strong decline of total N with altitudinal zones was also found for topsoils (Appendix B). Merely for Ae horizons we did not find an altitudinal decrease with elevation.

Total phosphorus

Total P is highest in SB, followed by litter, and declines with soil depth (Appendix A). The strongest correlation between total P and elevation (m a.s.l.) exists for SB, followed by litter (2013: r = -0.57), and Of layers (2013: r = -0.37, 2014: -0.48). No significant correlations were found for soil horizons, where P does not change much with elevation.

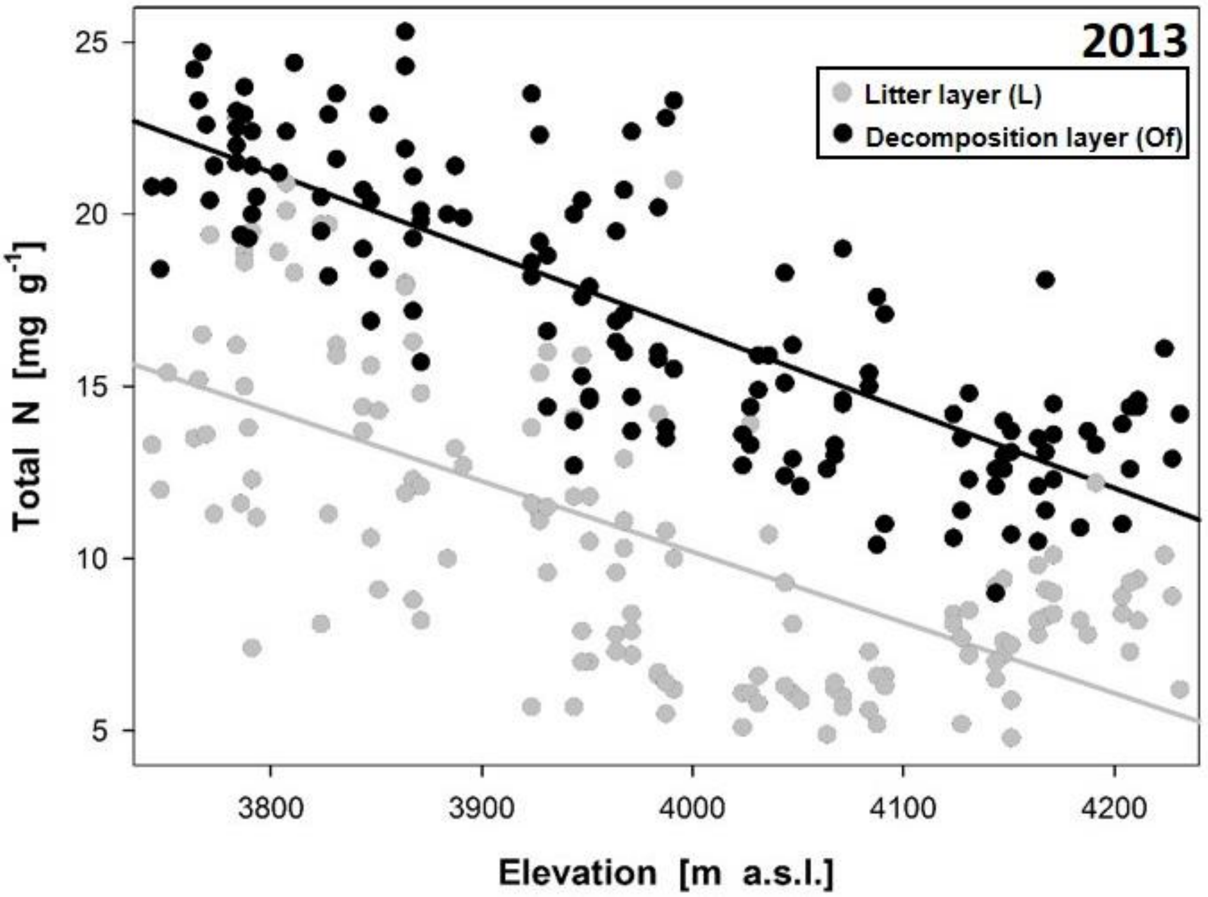

Fig. 3. Negative linear correlations between total N [mg g^{-1}] in litter layers (grey) and decomposition layers (black), and elevation [m a.s.l.] in 2013.

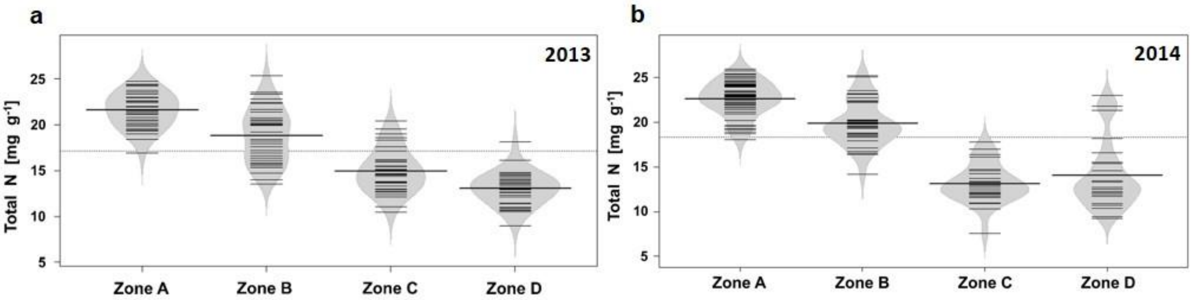

Fig. 4. Total N concentrations (Of samples) in zones A – D in 2013 (**a**, n= 146) and 2014 (**b**, n= 126). Each thin line represents a single value. Means of classes are depicted as thick black lines, estimated densities of distributions as grey areas, and means of all values as dotted grey lines.

Cation exchange capacity and base saturation

Soils show low Na^+ concentrations with a relative amount of 45 % (2013) and 59 % (2014) below the limit of determination. K^+, Mg^{2+}, and Ca^{2+} decline from Of to topsoils and Ae, respectively. Concentrations enrich slightly in Bh, and drop again in Bs (except for Ca in 2014, Appendix A). Accumulation in Bh in relation to Ae varies between 10 % (K^+), 75 % (Mg^{2+}) and 193 % (Ca^{2+}) (2014: 6 %, 32 %, 206 %). Fe and Al decline distinctly from Of and topsoils to Ae, but strongly rise again in Bh and Bs. Calculated H^+-ions are highest in topsoils and decrease with soil depth. CEC is highest in Of, decreases in topsoils and Ae, rises strongly in Bh, and drops again in Bs. Base saturation declines from Of to Bh, and increases slightly in Bs (Appendix A). In Of, we found a significant decline with elevation (m a.s.l.) for K (2013: r = -0.39, 2014: r = -0.66) and Mg (-0.50, -0.58), with considerable differences of K between zones AB, and CD (Appendix B). Mg in Of decreases continuously with altitudinal zones. A similar distribution was detected for litter K and Mg. In topsoils, Mg is lowest in D and highest in C. Hence, we did not find continuously decreasing mean values of altitudinal zones, which holds true for K (Appendix B). Our results do not show any significant correlation between elevation and exchangeable cations Ca^{2+}, Mn^{2+}, Fe^{3+}, Al^{3+}, and H^+ (each $R^2 \leq 0.06$). Overall, CEC decreases significantly with elevation in Of only ($R^2 = 0.13$).

Foliar nutrients

Foliar C does not change much with elevation, whereas foliar N declines significantly (Appendix C). Foliar N concentrations of *Rhododendron campanulatum* differ distinctly between closed forest (A, B), krummholz (C), and tundra (D), resulting in rising foliar C/N ratios with elevation (Appendix C). In particular, differences are remarkable between AB as compared to CD. Mean foliar N of *Abies spectabilis* decreases consistently with altitudinal zones, however, we found needle N in 2014 being highest in C. Within an altitudinal range of 460 m (3747 – 4207 m a.s.l.) a strong relative decrease of 28.36 % (2013, 2014: 27.09 %) is observed for foliar N of *Rhododendron campanulatum*. Mean foliar C, revealing the highest variance of various classes, differs barely between A and D (2013: 1.91 %, 2014: 3.20 %). Therefore, mean C/N ratios show a strong relative increase from A to D (2013: 41.71 %, 2014: 35.69 %). For the relation between C/N ratios of *Rhododendron campanulatum* foliage and elevation, we detected a coefficient of determination of 0.54 (r= 0.74) in 2013 and 0.57 (r= 0.76) in 2014.

The most distinct negative correlations with elevation were determined for P (2013: r = -0.44, 2014: r = -0.44) and K (-0.43, -0.58), while foliar Mg shows a weak to moderate relationship (-0.36, -0.21). Foliar P is similar in A and B (2013: mean A = 1.33 mg g^{-1}, B = 1.28 mg g^{-1}; 2014: A = 1.30 mg g^{-1}, B = 1.28 mg g^{-1}), but significantly higher compared to C (1.13 mg g^{-1}, 1.08 mg g^{-1}), and D (0.95 mg g^{-1}, 1.02 mg g^{-1}), respectively (Fig. 5). Similar differences were detected for foliar K between closed forest (2013: mean A = 5.88 mg g^{-1}, B = 5.55 mg g^{-1}; 2014: A = 5.65 mg g^{-1}, B = 5.07 mg g^{-1}), krummholz (C = 4.21 mg g^{-1}, 3.93 mg g^{-1}), and tundra (D = 4.01 mg g^{-1}, 3.33 mg g^{-1}). Foliar Mn of *Rhododendron campanulatum* is extraordinarily high in zone D (Fig. 5), exhibits a wide range (2013: 0.34 mg g^{-1} - 3.63 mg g^{-1}, 2014: 0.29 - 2.08 mg g^{-1}) and highest concentrations of all sample materials (mean = 1.87 mg g^{-1}, 0.73 mg g^{-1}). The same spatial pattern was determined for *Abies spectabilis*, however, with considerably lower Mn concentrations (2013: range = 0.07 - 1.34 mg g^{-1}, mean = 0.37 mg g^{-1}; 2014: 0.05 - 1.09 mg g^{-1}, mean = 0.32 mg g^{-1}).

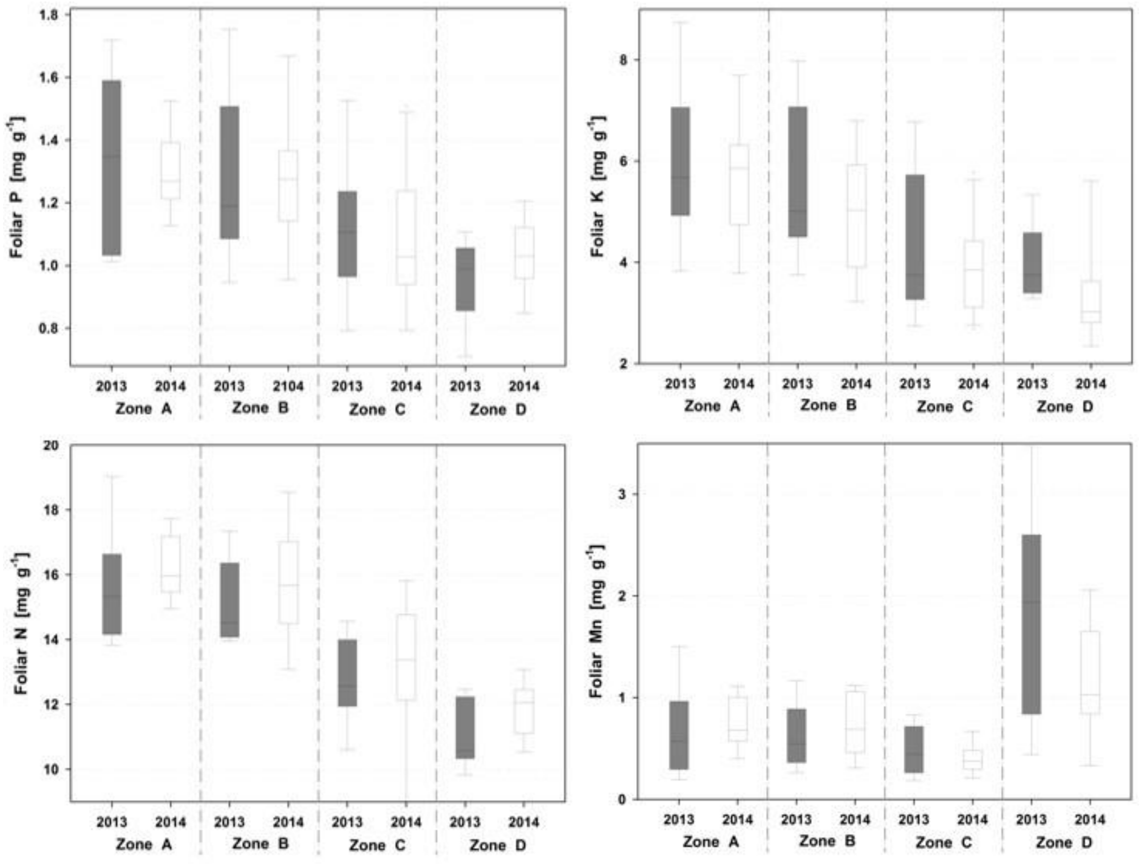

Fig. 5. Foliar P, K, N, and Mn concentrations (*Rhododendron campanulatum*) of altitudinal zones A - D in 2013 (grey) and 2014 (white).

Tree density and growth parameters

Tree species density increases distinctly from A (c. 1400 trees ha^{-1}) to B (c. 2100 trees ha^{-1}), and decreases slightly at the transition zone from B to C (about 2000 trees ha^{-1}). No tree-sized individuals (i.e. DBH > 7 cm) occur in zone D. Mean DBH of all species increases slightly from A to B, and shows a sharp decrease at the transition from B to C. Tree height decreases continuously from A to C.

Multiple linear regression analyses (MLR)

Due to a higher differentiation of sampling site elevations, we chose results of Of samples as the more suitable basis for models compared to topsoil samples. Models were created by an incremental exclusion of the respective least significant independent variable. Afterwards, we compared the resulting adjusted R² and p values (T-test) of each independent variable to determine the most valid models (Appendix D, shaded in grey). We conclude model mlr.Of_A6 to be the most valid model of decomposition layers, demonstrating only slight differences in adjusted R² compared to mlr.Of_A7, but featuring less variables and higher significances of single variables.

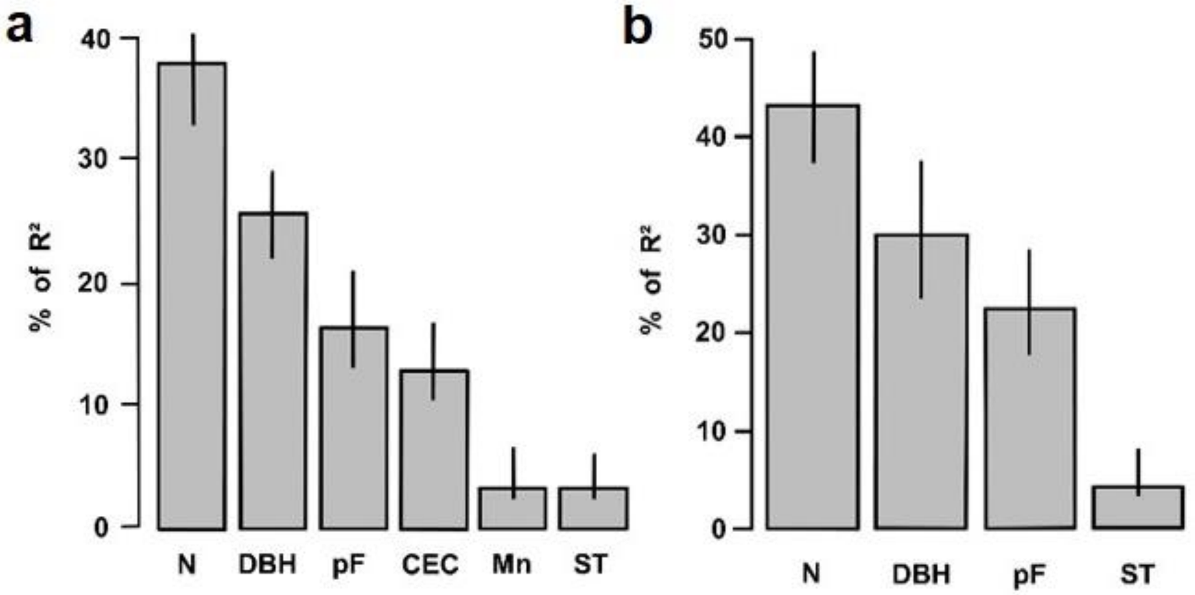

Fig. 6. Relative importance of variables for modelled elevation of model mlr.Of_A6 **(a)** and model mlr.Of_E4 **(b)**.

Relative importance of independent variables is demonstrated with 95 bootstrap confidence intervals by means of the *relaimpo* package (Grömping 2006) to quantify the relative contribution of each factor to the model explanatory value (Fig. 6). Therefore, the method LMG is conducted using sequential sums of squares from the linear model and averages over all orderings of regressors. For the model mlr.Of_A6, the independent variables N (37.95 %), DBH (25.81 %), pF (16.50 %), CEC (13.06 %), Mn (3.41 %), and ST (3.29 %) are most suitable for an approximation of the elevation of sampling sites (Fig. 6a). R^2 is 98.46 %, metrics are normalised to a sum of 100 %. The models mlr.Of_A12 – A1 are constructed by using plot-wise mean elevations of vegetation-related factors. Contrastingly, resulting models mlr.Of_E7 – E1 are achieved by assigning elevation of sampled trees to the respective elevation of closest sampling site of respective decomposition layers. As a result, data sets N, DBH, pF, and ST are best suitable to conduct most significant model of the elevation (Fig. 6b), featuring an adjusted R^2 of 0.73. A repetition of MLR for Of samples in 2014 revealed similar findings, concerning the resulting factors of most valid models, however, air temperature gains in importance.

Discussion

Pedogenic processes

The main pedogenic process is podzolisation, which is also reported from other treeline ecotones (Righi and Lorphelin 1987; Stützer 1999, Stöhr 2007). High precipitation and high water conductivity of sandy soils favour an eluviation of organic acids by soil water and adsorption processes from topsoils to subsoils forming soluble complexes with Al and Fe as known from podzolization processes elsewhere (cf. Anderson et al. 1982; Lundström et al. 2000; Buurman and Jongmans 2005). Our findings support that podzols feature a scarcity of N, K, and P availability. Soil acidification and Al and Fe excess in the lower subsoils, lead to a restricted nutrient uptake due to a poor replacement of base cations. Nutrient deficiency and high skeleton fractions of Ae horizons lead to a constrained fine root growth in subsoils, and a growing dependence on nutrient availability in topsoils and Of. Thus, plant nutrition most likely is coupled to a recycling of litter nutrients and does not depend on subsequent supply of nutrients from the mineral soil.

Soil nutrient limitation

Similar N values are reported from Alaska (Loomis et al. 2006). At least for topsoils, Garkoti and Singh (1994), Huber et al. (2007), Liptzin and Seastedt (2009), and Liptzin et al. (2012) detected even lower N values in different ecozones. In Rolwaling, no altitudinal trend is visible for L, Of, and soil C. Thus, significantly increasing C/N ratios indicate decreasing soil N availability with elevation. A similar finding is reported from Thébault et al. (2014) in Patagonia, Chile. They suggest tree growth limitation being the result of a competition between trees and soil microbial communities for low temperature limited soil inorganic N. In contrast, lower soil N availability with elevation in a treeline ecotone in Alaska is assumed being the consequence of limited microbial activity at low soil temperatures and in periodically wet soils (McNown and Sullivan 2013). Considerable narrower soil C/N ratios compared to our findings were found in podzols at the treeline in Norway (Stützer 1999) and in the Indian Himalaya (Garkoti and Singh 1994). A decrease of total soil N with elevation is also described by other studies from different ecozones (e.g., Sveinbjörnsson 2000; Köhler et al. 2006; Loomis et al. 2006; Huber et al. 2007). Loomis et al. (2006) found soil N distribution to be related to soil moisture, Köhler et al. (2006) assume drought and heat stress rather than nutrient limitation being responsible for treeline position. Increasing soil N with elevation was found in a treeline ecotone in Nepal (Shrestha et al. 2007). Higher total soil N was measured in the krummholz zone compared to the forest below and tundra above in the Rocky Mountains, Colorado (Liptzin et al. 2012) assuming the krummholz areas to be nutrient accumulation zones as a result of tree-wind interactions.

Total soil P in the study area is very low compared to data from other studies (e.g., Garkoti and Singh 1994; Shiels and Sanford 2001; Liptzin et al. 2012). We found P in Of and L to decrease with elevation. In the other horizons, however, P rather remained stable. This contradicts the result of Liptzin et al. (2012), who detected highest total and plant-available P in the krummholz zone compared to forest and tundra. Plant-available P did not change with elevation on Tenerife (Köhler et al. 2006). Our results show lower concentrations of exchangeable cations compared to other studies for K^+, Mg^{2+}, and Ca^{2+} (Garkoti and Singh 1994, Köhler et al. 2006; Liptzin and Seastedt 2009). Similar to our results, a decrease of soil K and Mg ions with elevation is reported from Tenerife (Köhler et al. 2006). A consistent soil K distribution with elevation was found in India (Garkoti and Singh 1994). For soil K, the same was detected in Colorado (Liptzin and Seastedt 2009), whereas soil Mg slightly increased with elevation.

Limited nutrient supply of soil N, K, Mg, and P (P in L and Of only) becomes more intense with elevation, and here in particular in the krummholz and beyond. This intense decline in nutrient supply spatially coincides with abrupt changes in vegetation composition and growth parameters (cf. Schwab et al. 2016). Further, very acid soil conditions and low base saturation of soils demonstrate a lack of soil nutrients. Higher C/N ratios with elevation may reflect a low organic matter turnover in soils. Therefore, we assume low soil nutrient availability to affect tree growth in the Rolwaling treeline ecotone.

Foliar nutrient concentrations

Our results suggest macronutrient deficiency also in foliage. According to defined thresholds of five representative European main tree species, 83 % (2014: 90 %) of *Rhododendron campanulatum* samples show foliar K concentrations below a threshold of 6.34 mg g^{-1} (Braun and Flückiger 2013). Foliar K was also observed to decline with elevation at the treeline in India (Garkoti and Singh 1994) and in Ecuador (Soethe et al. 2008). Köhler et al. (2006) detected decreasing foliar K and Mg with elevation in some species on Tenerife. K deficiency may have a crucial impact on the water balance, leading more quickly to dehydration and frost damages (Braun and Flückiger 2009). Macek et al. (2012) reported from decreasing foliar Mg with elevation in vascular plants within a treeline ecotone in northwest Himalaya. A decline in foliar Mg was also identified by Friedland et al. (1988) in red spruces. About 75 % of Rhododendron leaves indicate P deficiency. Similarly, decreasing foliar P with elevation is reported from varying ecozones and altitudes (Garkoti and Singh 1994; Richardson 2004; Soethe et al. 2008; Macek et al. 2012; Zhao et al. 2014). Similar trends with elevation and distinct relationships between soil nutrient availability and leave nutrient concentrations of N, Mg, K, and partly P indicate the importance of macronutrient cycling on vegetation composition at an ecosystem scale and a potential nutrient limitation of trees within the treeline ecotone.

Foliar N in the study area is very low in comparison to foliar deficiency ranges of European tree species (e.g., Göttlein et al. 2011, Mellert and Göttlein 2012, Braun and Flückiger 2013). Our results are in line with findings from treeline ecotones worldwide (e.g. De Lillis et al. 2004; Körner 2012 Li et al. 2008; McNown and Sullivan 2013), however, means are lower than found in most of these studies. Declining foliar N with elevation in treeline ecotones is also reported by Garkoti and Singh (1994) in India, Richardson et al. (2004) in Colorado, and McNown and Sullivan (2013) in Alaska. The same was detected by Soethe et al. (2008) in Ecuador and by Zhao et al. (2014) in China, however, not directly at treeline elevation. In contrast, Hoch and Körner (2005) reported from higher foliar N in treeline trees compared to lower elevation sites in Bolivia. A worldwide study from Körner (1989) shows increasing foliar N of herbaceous plants with elevation, whereas foliar N contents of evergreen woody species remain stable. Similarly, Birmann and Körner (2009) found no differences in needle N with elevation in the Alps. Overall, we did not find any foliar nutrient to increase with elevation, besides Mn. Therefore, our results contradict the paradigm of increasing foliar nutrient concentrations with elevation, and the view that plants in cold growth environments are adapted by sustaining high soil and foliar nutrient concentrations (e.g., Körner 1989, 2012; Weih and Karlsson 2001; Reich and Oleksyn 2004).

Foliar Mn excess above treeline

We assume a toxic effect of high foliar Mn above the krummholz zone: mean foliar Mn concentrations of 1.87 mg g^{-1} (2014: 0.73 mg g^{-1}) are clearly higher than defined thresholds for Mn toxicity (> 0.02 to 0.5 mg g^{-1}; Liu et al. 2010, Madejón et al. 2005) and partly higher than 0.02 to 1.5 mg g^{-1} defined for European tree species (Braun and Flückiger 2009). Typical symptoms of Mn toxicity are visible on leaves of *Rhododendron campanulatum* at high elevation sites, such as brown stains on mature leaves, deformation of young leaves, chlorophyll deficiency, and wrinkled leaf margins (Wissemeier and Horst 1992; González et al. 1998). An essential condition for the strong Mn accumulation in leaves is the very high soil acidity, since Mn becomes strongly plant available under these conditions. Intense solar radiation due to a missing protective vegetation cover in zone D may be an important factor for accumulation of Mn in leaves. Previous studies demonstrated enhanced Mn accumulations in leaves exposed to higher light intensities (Elamin and Wilcox 1986; Horst 1988). It was also observed that more Mn accumulates in sun leaves than in shade leaves (Haas et al. 1968, McCain and Markley 1989). Finally, drought stress - which occurs especially during spring months in the study area (Schickhoff et al. 2015) - inhibits photosynthesis in plants by leading to closed stomata and damaged photosynthetic apparatus, thus affects the Mn concentrations (Gavalas and Clark 1971).

Limiting factors on tree growth

The modelled elevation of experimental plots is most suitable by using the factors N, DBH, ST, and pF, and partly CEC and Mn. N is the most significant variable of all models, and is therefore supposed to play a major role for the inhibition of tree growth establishment at high elevation sites. Differences in soil moisture conditions of sampling sites are associated with high solar radiation in zone D, differences in vegetation composition and number of individuals. We assume soil moisture being an important factor at the onset and end of growing season: seasonal changes in precipitation and frozen soils directly influence vegetation pattern by causing drought stress and therefore inhibit tree growth at high elevation sites. The calculated models show significant differences in macronutrient concentrations within a small area and feature strong validities and strong altitude-dependence of variables. The great variability of vegetation, climate and soil properties and interactions between variables indicate that varying site conditions (e.g., soil N, CEC, soil moisture) play a crucial role for tree growth at local scale. A further integration of climatic and vegetation-related datasets, as well as the inclusion of temporal changes would improve the accuracy of resulting models.

Conclusions

Our findings indicate nutrient deficiency in soils and trees of the Rolwaling treeline ecotone. Decreasing concentrations of N, Mg, K, and P with elevation suggest limited tree growth due to insufficient soil nutrient supply. Plant nutrition is most likely coupled to a recycling of litter nutrients and does not depend on subsequent supply of nutrients from the mineral soil. Besides, foliar Mn excess above treeline is supposed to play a role in constraining tree growth and seedling establishment. MLR analyses indicate multilateral interactions and a high variability of essential nutrients within the treeline ecotone, as well as a high influence of soil nutrient supply, soil temperature and soil moisture on local tree growth limitation. We assume vegetation composition and treeline position being strongly affected by nutrient limitation, which in turn, is governed by low soil temperatures and influenced by soil moisture conditions.

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Appendices

Appendix S1. Mean values of soil and foliar nutrient data of different sampling material in 2013 and 2014.

Year	**Sample material**	**C_t [mg g^{-1}]**	**N_t [mg g^{-1}]**	**C/N**	**P_t [mg g^{-1}]**	**pH [KCl]**	**Na[a,b]**	**K[a,b]**	**Mg[a,b]**	**Ca[a,b]**	**Mn[a,b]**	**Fe[a,b]**	**Al[a,b]**	**H[b]**	**CEC[b]**	**BS [%]**
2013	SB (n=115)	486.3	13.8	35.81	1.21	na	0.02[a]	4.92[a]	1.47[a]	6.71[a]	0.71[a]	0.07[a]	0.16[a]	na	na	na
	L (n =146)	463.2	10.7	50.99	0.71	na	0.05[a]	1.93[a]	1.67[a]	10.49[a]	0.91[a]	0.43[a]	0.67[a]	na	na	na
	Of (n=145)	420.3	17.1	25.90	0.16	na	0.33[b]	2.95[b]	5.93[b]	25.61[b]	1.42[b]	0.35[b]	1.16[b]	1.87[b]	39.62[b]	85.58
	Ah (n = 48)	216.8	11.3	19.70	0.0417	2.95	0.03[b]	0.52[b]	1.74[b]	6.30[b]	0.41[b]	0.50[b]	3.83[b]	2.45[b]	15.76[b]	50.38
	Ae (n =52)	33.8	1.7	19.82	0.0050	3.18	0.01[b]	0.10[b]	0.20[b]	0.43[b]	0.01[b]	0.19[b]	1.80[b]	0.65[b]	3.39[b]	23.76
	Bh (n = 21)	124.3	5.4	23.36	0.0028	3.43	0.02[b]	0.11[b]	0.35[b]	1.26[b]	0.01[b]	1.10[b]	13.30[b]	0.45[b]	16.61[b]	10.58
	Bs (n =36)	60.8	2.4	25.22	0.0006	3.90	0.01[b]	0.05[b]	0.16[b]	0.77[b]	0.01[b]	0.36[b]	5.42[b]	0.11[b]	6.88	13.66
2014	SB (n =129)	476.4	14.6	32.61	1.20	na	0.02[a]	4.71[a]	1.56[a]	6.88[a]	0.62[a]	0.10[a]	0.20[a]	na	na	na
	L (n = 148)	465.8	11.0	49.73	na	na	na	na	na	na	na	na	na	na	na	na
	Of (n =125)	420.9	18.3	23.00	0.18	na	0.05[b]	2.42[b]	6.76[b]	28.26[b]	2.00[b]	0.10[b]	0.47[b]	1.09[b]	41.15[b]	89.42
	Ah (n = 54)	225.8	11.6	19.99	0.0346	na	0.02[b]	0.73[b]	1.94[b]	6.22[b]	0.15[b]	0.57[b]	3.77[b]	2.71[b]	16.10[b]	49.54
	Ae (n = 48)	54.4	2.6	20.92	0.0075	na	0.01[b]	0.17[b]	0.31[b]	0.75[b]	0.01[b]	0.20[b]	1.77[b]	1.03[b]	4.25[b]	25.53
	Bh (n = 30)	107.0	4.8	22.29	0.0021	na	0.01[b]	0.18[b]	0.41[b]	1.55[b]	0.03[b]	0.98[b]	10.37[b]	0.35[b]	13.89[b]	16.33
	Bs (n = 24)	63.7	2.5	25.48	0.0045	na	0.01[b]	0.16[b]	0.36[b]	1.63[b]	0.03[b]	0.45[b]	5.80[b]	0.24[b]	8.67[b]	17.15

[a] Concentrations of Na, K, Mg, Ca, Mn, Fe, and Al in [mg g^{-1}]

[b] Exchangeable cations Na^+, K^+, Mg^{2+}, Ca^{2+}, Mn^{2+}, Fe^{3+}, Al^{3+}, and calculated values of H^+-ions and effective cation exchange capacity (CEC) in [cmol kg^{-1}]

BS = base saturation

Appendix S2. Soil nutrient data (L, Of, Ah) in altitudinal zones A - D.

Sample material	**Zone**	**C_t [mg g^{-1}]**		**N_t [mg g^{-1}]**		**C/N**		**P_t [mg g^{-1}]**		**$K^{a,b}$**		**$Mg^{a,b}$**	
		2013	**2014**	**2013**	**2014**	**2013**	**2014**	**2013**	**2014**	**2013**	**2014**	**2013**	**2014**
L	A	45.36	46.86	15.48	13.58	31.62	34.50	1.04	na	3.29^a	na	2.27^a	na
	B	46.42	46.74	11.39	11.42	44.59	40.93	0.76	na	2.00^a	na	1.94^a	na
	C	46.14	46.48	7.44	7.72	66.96	60.24	0.47	na	1.05^a	na	1.49^a	na
	D	47.42	47.48	8.20	8.91	60.77	53.30	0.53	na	1.26^a	na	0.95^a	na
Of	A	42.11	42.72	21.45	22.50	19.76	18.98	0.19	0.25	3.53^b	3.40^b	7.65^b	8.68^b
	B	42.71	41.65	18.76	19.70	23.28	21.10	0.18	0.18	3.64^b	2.20^b	6.30^b	7.27^b
	C	42.64	41.97	14.93	13.30	29.28	31.58	0.13	0.11	2.42^b	1.40^b	5.57^b	4.75^b
	D	40.52	41.01	13.02	13.90	31.57	29.52	0.14	0.11	1.79^b	1.88^b	4.03^b	4.56^b
Ah	A	20.42	25.20	12.11	14.64	16.86	17.21	0.0362	0.0362	0.49^b	0.86^b	1.68^b	2.09^b
	B	23.50	24.40	12.98	12.42	18.11	19.64	0.0391	0.0439	0.47^b	0.69^b	1.78^b	2.00^b
	C	24.51	27.45	11.41	12.04	21.48	22.88	0.0470	0.0380	0.55^b	0.74^b	2.11^b	2.41^b
	D	17.10	18.58	7.39	8.60	23.14	21.67	0.0356	0.0202	0.55^b	0.60^b	1.11^b	1.27^b

[a] Concentrations of K and Mg in [mg g^{-1}]

[b] Exchangeable cations K^+ and Mg^{2+} in [cmol kg^{-1}]

Appendix S3. Mean foliar C, N concentrations, and C/N ratios of altitudinal zones A-D of tree species *Rhododendron campanulatum* and *Abies spectabilis* in 2013 and 2014.

Rhododendron campanulatum	**Zone**	**C [mg g^{-1}]**	**N [mg g^{-1}]**	**C/N**	***Abies spectabilis***	**Zone**	**C [mg g^{-1}]**	**N [mg g^{-1}]**	**C/N**
2013	A	474.99	15.62	30.71	**2013**	A	484.21	14.17	34.59
n = 54	B	477.91	15.09	31.85	**n = 37**	B	482.01	13.63	35.83
	C	481.63	12.76	38.20		C	482.60	13.25	36.67
	D	484.07	11.19	43.52		D	481.54	12.56	38.58
2014	A	469.75	16.24	29.03	**2014**	A	470.80	14.15	33.63
n = 63	B	461.90	15.71	29.77	**n = 34**	B	455.84	14.28	32.50
	C	454.70	13.52	34.13		C	483.51	15.04	33.59
	D	464.50	11.84	39.39		D	471.41	11.32	41.65

Appendix S4. Comparison and selection of MLR models for the approximation of elevation (decomposition layer samples) in 2013.

Model name	**Number of indep. variables**	**Adjusted R^2 of model**	**Number of p-values of T-tests of independent variables**					**Independent variables**[a]
			0 - 0.001	**0.001 -0.01**	**0.01 - 0.05**	**0.05- 0.1**	**0.1 - 1**	
mlr.of_A12	12	0.7815	5	1	1	5	0	N, DBH, Mn, CEC, ST, pF, SL, CD2, CD1, Temp, C, H
mlr.of_A11	11	0.7784	4	2	0	4	1	N, DBH, Mn, CEC, ST, pF, SL, CD2, CD1, Temp, C
mlr.of_A9	9	0.7732	4	2	1	1	1	N, DBH, Mn, CEC, ST, pF, SL, CD2, CD1
mlr.of_A8	8	0.7705	4	2	1	0	1	N, DBH, Mn, CEC, ST, pF, SL, CD2
mlr.of_A7	**7**	**0.7687**	4	2	1	0	0	**N, DBH, Mn, CEC, ST, pF, SL**
mlr.of_A6	**6**	**0.7604**	3	3	0	0	0	**N, DBH, Mn, CEC, ST, pF**
mlr.of_A5	5	0.7488	4	0	0	0	1	N, DBH, Mn, CEC, ST
mlr.of_A4	**4**	**0.7465**	4	0	0	0	0	**N, DBH, Mn, CEC**
mlr.of_A3	3	0.7236	3	0	0	0	0	N, DBH, Mn
mlr.of_A2	2	0.7077	2	0	0	0	0	N, DBH
mlr.of_A1	1	0.6478	1	0	0	0	0	N
mlr.of_E7	7	0.7284	3	1	0	0	3	N, pF, ST, DBH, Temp, SL, Fe
mlr.of_E6	6	0.7283	4	0	0	0	2	N, pF, ST, DBH, Temp, SL
mlr.of_E5	5	0.7270	4	0	0	0	1	N, pF, ST, DBH, Temp
mlr.of_E4	**4**	**0.7254**	**4**	**0**	**0**	**0**	**0**	**N, pF, ST, DBH**
mlr.of_E3	**3**	**0.7033**	**3**	**0**	**0**	**0**	**0**	**N, pF, ST**
mlr.of_E2	2	0.6806	2	0	0	0	0	N, pF
mlr.of_E1	1	0.6478	1	0	0	0	0	N

[a] C – carbon, CD2 – crown diameter hillside, CDpar – crown diameter parallel, CEC- Cation exchange capacity, DBH – diameter at breast height, Fe – iron, H – hydrogen, Mn – manganese, pF – mean soil water tension (pF value), SL- Slope, ST - Soil temperature in 10 cm depth, Temp – Soil surface air temperature

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Do Himalayan treelines respond to recent climate change? An evaluation of sensitivity indicators

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Abstract

Climate warming is expected to induce treelines to advance to higher elevations. Empirical studies in diverse mountain ranges, however, give evidence of both advancing alpine treelines and rather insignificant responses. The inconsistency of findings suggests distinct differences in the sensitivity of global treelines to recent climate change. It is still unclear where Himalayan treeline ecotones are located along the response gradient from rapid dynamics to apparently complete inertia. This paper reviews the current state of knowledge regarding sensitivity and response of Himalayan treelines to climate warming, based on extensive field observations, published results in the widely scattered literature, and novel data from ongoing research of the present authors.

Several sensitivity indicators such as treeline type, treeline form, seed-based regeneration, and growth patterns are evaluated. Since most Himalayan treelines are anthropogenically depressed, observed advances are largely the result of land use change. Near-natural treelines are usually krummholz treelines, which are relatively unresponsive to climate change. Nevertheless, intense recruitment of treeline trees suggests a great potential for future treeline advance. Competitive abilities of seedlings within krummholz thickets and dwarf scrub heaths will be a major source of variation in treeline dynamics. Tree growth–climate relationships show mature treeline trees to be responsive to temperature change, in particular in winter and pre-monsoon seasons. High pre-monsoon temperature trends will most likely drive tree growth performance in the western and central Himalaya. Ecological niche modelling suggests that bioclimatic conditions for a range expansion of treeline trees will be created during coming decades.

1 Introduction

Treeline advance to higher elevation results in substantial physiognomic, structural, and functional changes in mountain landscapes and ecosystems. Thus, sensitivity and response of alpine treelines to climate change is increasingly being discussed among scientists and by the general public (Holtmeier, 2009). Strong general links between climate parameters and treeline position and repeated climatically caused treeline fluctuations during the Holocene

(MacDonald et al., 2000; Tinner and Theurillat, 2003; Reasoner and Tinner, 2009) suggest treelines to be sensitive and useful indicators of climatic changes (cf. Slatyer and Noble, 1992; Kullman, 1998; Theurillat and Guisan, 2001; Grace et al., 2002; Fagre, 2009; Kullman and Öberg, 2009; Smith et al., 2009). Generally, global warming is expected to cause upper treelines to advance to higher elevations since, at a global scale; the position of natural alpine treelines is controlled mainly by heat deficiency, i.e. insufficient air and soil temperatures during growing season (Körner and Paulsen, 2004; Holtmeier and Broll, 2005, 2009; Holtmeier, 2009; Körner, 2012a; Paulsen and Körner, 2014). The general agreement of the thermal limitation of treeline positions 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, nutrient availability, soil moisture, species dispersal and recruitment, plant morphology, self-organization) influencing tree growth at its upper limit (e.g. Hoch et al., 2002; Smith et al., 2003; Dullinger et al., 2004; Holtmeier and Broll, 2007; Wieser, 2007, 2012; Bansal et al., 2011; Hoch and Körner, 2012; Körner, 2012a, b).

The current state of knowledge on treelines has been acquired by a wealth of research efforts that can be differentiated into two major conceptual approaches operating at different spatial scales (cf. Malanson et al., 2011). Studies exploring fundamental, global-scale causes of treelines (e.g. Körner, 1998), often characterized by a strong focus on limitations to tree growth from an ecophysiological perspective, can be referred to as the “global approach”. Other studies attempt to understand finer-scale (landscape-scale, local-scale) causes of treelines and variations in spatial and temporal patterns (e.g. Holtmeier, 2009). The focus here is on landscape patterns, in particular on the effects of topography and other site conditions and on treeline history. Such studies can be subsumed under the term “landscape approach”. Both research lines have contributed significantly in recent years to answering the key question of treeline response to recent climate change. This response will not linearly follow altitudinal shifts of isotherms but rather vary according to the interaction of broad-scale controls (global/regional temperature) and fine-scale modulators of treeline patterns (Holtmeier and Broll, 2005, 2007, 2009; Holtmeier, 2009; Malanson et al., 2011). It has thus become routine to take the scale dependency of drivers controlling treeline patterns into account (Malanson et al., 2007; Danby, 2011). As treeline heterogeneity increases from global/regional to landscape and local scales, an increasing number of factors and their interactions have to be considered. Effects of varying topography on local site conditions, spatially and temporally variable soil physical and chemical properties, after-effects of historical disturbances (extreme events, fire, insect pests, human impact, etc.), demographic processes, and species-specific traits and/or biotic interactions and feedback systems may override or overcompensate for the impact of higher average temperatures. It has also to be emphasized that various treeline-forming species will have different growth and regeneration responses to a changing climate. In the long term, treelines will advance under continued global warming, but not in a closed front parallel to the shift of an isotherm (Holtmeier and Broll, 2005, 2007; Malanson et al., 2011; Körner, 2012a).

The response of treelines to observed climate warming is indeed inconsistent. A recent meta-analysis of treeline response to climate warming, based on a global data set of 166 sites for which treeline dynamics had been reported since AD1900, showed advancing treelines at 52 % of the sites, while 47 % did not show any elevational shifts and only 1 % showed treeline recession (Harsch et al., 2009). Treelines with higher rates of winter warming were more likely to show advance. At many treeline sites in mountain regions settled long ago, however, effects of climate warming interfere with those of land use changes (e.g. Bolli et al., 2006; Vittoz et al., 2008; Rössler et al., 2008). Gehrig-Fasel et al. (2007) found land abandonment to be the most dominant driver for recent treeline shifts in the Swiss Alps, and attributed only a small fraction of upward shifts to climate change. Some studies documented substantial treeline advances during the twentieth century. Most authors trace it back to climate warming, not always disentangling the effects of land use and climate change. Treeline advances of up to 70–100m (altitudinal metres) were reported from several mountain ranges in the Northern Hemisphere and attributed to climate changes (e.g. Danby and Hik, 2007; Kharuk et al., 2010; Moiseev et al., 2010). Kullman and Öberg (2009) quantified a maximum treeline advance of 200m in the southern Swedish Scandes. Other recent empirical studies reported enhanced tree growth, tree establishment, and infilling of gaps within the treeline ecotone during recent decades (e.g. Rolland et al., 1998; Camarero and Gutiérrez, 2004; Daniels and Veblen, 2004; Dalen and Hofgaard, 2005; Wang et al., 2006; Kullman, 2007; Roush et al., 2007; Akatov, 2009; Liang et al., 2011). Locally increasing numbers of tree seedlings above the current upper tree limit, occasionally far above, are reported from many mountain ranges (e.g. Kullman, 2008; Hofgaard et al., 2009).

The above-cited treeline studies give evidence of both advancing alpine treelines and rather insignificant treeline responses to climate warming. The inconsistency of findings suggests significantly differing sensitivities of global treelines to climate changes. It is known that climate operates at a broad spatial scale and typically exerts a top-down control on local ecological patterns and processes at the treeline (Batllori and Gutiérrez, 2008; Elliott, 2011). It is widely unknown, however, how local-scale site conditions (abiotic site factors, plant interactions associated with facilitation, competition, feedback systems) can modify the treeline response to region-wide climate warming inputs. Thus, it remains unclear how abiotic and biotic factors and processes interact to govern sensitivity and response of the treeline at landscape and local scales (cf. Holtmeier and Broll, 2007; Malanson et al., 2007; Batllori et al., 2009; Smith et al., 2009). Recent studies based on a global treeline data set suggest a close link between treeline form (spatial pattern) and dynamics. Harsch et al. (2009) and Harsch and Bader (2011) consider treeline form (diffuse, abrupt, island, krummholz) to be an indicator of controlling mechanisms and response to climate change. They found the majority of diffuse treelines and about onethird of krummholz treelines to be advancing, and abrupt and island treelines to be rather stable. The disjunction of mechanisms and environmental conditions primarily associated with different treeline forms seems to explain this pattern. However, given the nonlinear responses to climate warming caused by various local-scale modulators and their interactions, numerous limitations remain in the use of treeline form to predict treeline dynamics. In order to analyse the role of local-scale processes in mediating the broader-scale climate inputs, and to improve the model-based prediction ability regarding changing spatial treeline patterns, complex research approaches at local and landscape scales and in different treeline environments are required. These should focus on treelines which do not show substantial treeline depressions as a result of human impact.

Identified research deficits regarding the sensitivity and response of alpine treelines to climate change apply in particular to the Himalaya. While numerous treeline research programmes have been carried out in European and North American mountains, related research in the Himalaya is still in the early stages. A recent review of geographical and ecological aspects of the treeline ecotone in the Himalayan mountain system revealed considerable research deficits, in particular with regard to responses to climate change (Schickhoff, 2005). Considering the sensitivity of mountain biota and ecosystems to environmental change on a global scale (e.g. Grabherr et al., 2010; Schickhoff, 2011; Engler et al., 2011; Laurance et al., 2011; Gottfried et al., 2012) and on a Himalayan scale (Xu et al., 2009; Shrestha et al., 2012; Telwala et al., 2013; Aryal et al., 2014), substantial effects on Himalayan treeline ecotones are to be expected. This paper reviews the current state of knowledge regarding sensitivity and response of Himalayan treelines to climate warming, presents novel data from ongoing studies, provides explanations for present findings, and conducts a globally comparative evaluation of Himalayan response patterns.

2 Geography and ecology of Himalayan treeline ecotones

The Himalayan mountain system occupies a vast territory, extending from Afghanistan in the northwest (ca. 36°N and 70°E) to Yunnan in the southeast (ca. 26°N and 100°E). It encompasses a geographic relief of enormous dimensions, including the Tibetan Plateau in the north, all 14 of earth’s summits above 8000 m, and the outer foothills of the Indo-Gangetic Plain in the south. As indicated by the vegetation of its immediate forelands, the Himalaya crosses several horizontal climatic zones. Subtropical semi-desert and thorn steppe formations in the northwest are replaced by tropical evergreen rainforests in the southeast along a pronounced gradient of increasing humidity. A steep gradient of decreasing humidity is developed across the mountain system from south to north. The staggered mountain ranges act as climatic barrier to moisture-bearing monsoonal air masses, and cause a sharp decline in precipitation in peripheral–central direction. Along this gradient the densely forested Himalayan south slope strongly contrasts with steppe lands on the Tibetan Plateau.

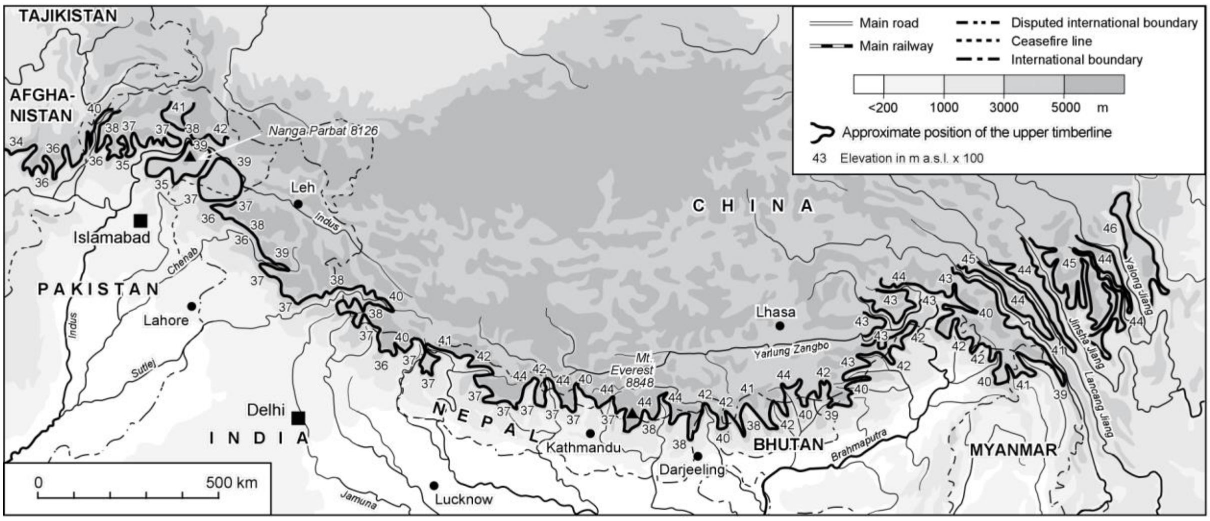

Figure 1. Altitudinal position of alpine treeline in the Himalayan mountain system (north-facing slopes) (modified after Schickhoff, 2005).

According to the complex three-dimensional geoecological differentiation with a high diversity of hygric, thermal, edaphic, and biotic conditions, Himalayan treeline ecotones show considerable differences in altitudinal position as well as in physiognomy and species composition (Schickhoff, 2005). Along the two gradients described above, treeline elevations increase in accordance with increasing higher mean annual temperatures at same altitudes (Fig. 1). Along the mountain arc from northwest to southeast, the latitude-related temperature increase causes an upward shift of treelines of about 1000 m. At the northwestern range limit of monsoon-dependent Himalayan forests (central Hindu Kush), treeline elevations reach 3400–3600 m (north-facing slopes). In the northern mountain ranges of Yunnan and in SE Tibet in the southeast, the upper limit of tree growth attains elevations of ca. 4600 m in northern aspects. The more or less linear ascent of treeline elevations along the peripheral–central gradient from the Himalayan south slope to the Tibetan highlands, which can be up to 600 m, is modified at single high-mountain massifs (e.g. Dhaulagiri and Annapurna Himal) with treelines located at higher altitudes than further north. Like in other subtropical high mountains, treelines considerably vary in their altitudinal position according to aspect and related topoclimatic differences. Under natural conditions, treelines are usually developed at significantly higher elevations on south-facing slopes. Anthropogenic disturbances have blurred this general pattern to a locally different extent since utilization pressure in southern aspects is disproportionately higher (Schickhoff, 2005).

Interestingly, mean summer temperatures are significantly higher in the more continental NW; the treeline, however, is developed at distinctly lower elevations (Fig. 1). Extremely low winter temperatures with a long snow cover duration and shorter growing seasons obviously overcompensate for the effects of favourable summer temperatures. Moreover, the internal preparedness of the predominantly deciduous treeline tree species in the far NW such as *Betula utilis*, *Salix* spp., and hardy conifers to build new tissue and accumulate dry matter is delayed compared to the evergreen *Rhododendron* species at treelines in the more maritime SE. Increasing treeline elevations along the peripheral–central gradient (see Fig. 1) are related to the combined effects of mass elevation and continentality. As in other extensive mountain massifs, the inner Himalayan highlands provide elevated heating surfaces, leading to positive thermal anomalies compared to marginal ranges or free air and causing altitudinal vegetation limits to rise (cf. Flohn, 1968; Yao and Zhang, 2014). The continentality effect exerts an even stronger influence on treeline elevations (Schickhoff, 2005). Decreasing cloudiness and precipitation, coupled with higher irradiation and sunshine duration, earlier snow melt, and higher soil temperatures, results in higher temperature sums and a prolonged growing season. The peripheral–central gradient culminates in SE Tibet, where *Juniperus tibetica* forms the most elevated treeline in the Northern Hemisphere at an altitude of 4900 m (Miehe et al., 2007).

The physiognomy of Himalayan treeline ecotones greatly varies depending on slope aspect. North-facing slopes exhibit a more or less homogeneous physiognomic pattern, with closed high coniferous forests giving way to mediumsized broadleaved tree stands and finally to a krummholz belt, interspersed with single, small upright trees (Fig. 2). Remnant forest stands on south-facing slopes are usually open coniferous forests that dissolve into isolated patches or single crippled trees over a broad altitudinal zone (Fig. 3). North- and south-facing slopes also show pronounced differences with regard to treeline-forming tree species. In the NW and W Himalaya, montane and subalpine vegetation in northern aspects primarily consists of coniferous forests (*Abies pindrow, Pinus wallichiana, Picea smithiana, Cedrus deodara*) which show an increasing proportion of birch (*Betula utilis*) in the upper subalpine belt and finally turn into a narrow band of more or less pure birch stands. *Rhododendron campanulatum*, *Sorbus* spp., and *Salix* spp. are principal understory species. Further upslope, *Betula utilis* and *Sorbus* spp. grow scattered in a crippled growth form and merge into a *Rhododendron* and/or *Salix* krummholz belt, which delimits the treeline ecotone and marks the transition to the alpine belt. Along the northwest–southeast gradient, increasingly more maritime climatic conditions with strongly decreasing winter cold and higher monsoonal humidity levels increase the competitiveness of evergreen trees and large shrubs of the genus *Rhododendron* (*Rh. campanulatum, Rh. barbatum, Rh. wightii, Rh. fulgens, Rh. lanatum, Rh. bhutanense*, among others), which replace the deciduous birch belt in the E Himalaya. Concomitantly, the hardy fir, spruce, and pine species give way to other coniferous trees in high-altitude forests in Nepal, Sikkim, and further to the east. Species such as *Abies spectabilis*, *Abies densa*, *Picea spinulosa*, and *Larix griffithiana* ascend from closed forests in the upper montane and lower subalpine belt into the Rhododendron-dominated treeline ecotone with uppermost *Rhododendron* stands turning into krummholz and *Rhododendron* dwarf shrubs further upslope (Miehe and Miehe, 2000; Miehe, 2004; Schickhoff, 2005).

Along the entire mountain arc, *Juniperus* spp. are the principal treeline tree species on south-facing slopes. Below the treeline ecotone, coniferous forests (mostly *Pinus wallichiana* forests, in more humid areas even *Abies* forests) cover southern aspects if they have not been transformed into grazing lands. Several juniper species (*Juniperus excelsa, J. semiglobosa, J. turkestanica, J. recurva, J. wallichiana, J. indica, J. tibetica*, among others) are able to grow as upright trees in the subalpine belt, forming stands of varying density.

Most common are very open woodlands, in particular in the NW Himalaya. In pasture areas, junipers often occur as single isolated individuals. South-facing slopes often lack a distinct and easily recognizable altitudinal zonation of vegetation mainly due to excessive human impact. Scattered junipers may change their growth form from tree to (dwarf) shrub with increasing altitude (e.g. *J. indica, J. recurva*), and are generally less suitable for the delimitation of treeline ecotones. The potential natural stand structure of juniper groves is hard to reconstruct since south-facing slopes are strongly modified by human impact for centuries, if not millennia (Miehe, 1990; Miehe and Miehe, 2000; Schickhoff, 2005).

Figure 2. Altitudinal zonation of a near-natural north-facing treeline in the central Himalaya: upper subalpine forests of *Abies spectabilis* and *Betula utilis* (leaves still unfolded) give way to *Rhododendron campanulatum* krummholz at ca. 4000 m, Rolwaling, Nepal (Schickhoff, 15 April 2013).

3 Regional climate change

The climate of the Himalayan Arc is triggered by the seasonal shift of the major pressure cells over Asia and the adjacent oceans and the accompanying change of large-scale circulation patterns, which lead to a distinct hygric seasonality, referred to as “monsoon”. Due to the strong establishment of the Asian Heat Low, the summer season is characterized by a southwesterly flow, originating over the Bay of Bengal, which advects moist air masses into the eastern Himalayas and leads to summer precipitation amounts of up to 5000 mm at the windward Himalayan slopes. A minor monsoonal current from the Arabian Sea transports moist air masses into the western part of the Himalaya. In contrast, the winter climate is determined by a uniform westerly flow. The upper tropospheric jet stream at the 200 hPa level determines the trajectories of extratropical western disturbances, which lead to occasional precipitation events, particularly in the western Himalaya (Böhner, 2006; Maussion et al., 2013). While the eastern Himalaya receives more than 80 % of the annual precipitation during summer season, the winter precipitation over the far western parts reaches up to 50 % of the annual amount. The transition seasons are characterized by mainly dry conditions throughout the Himalaya, although infrequent convective precipitation events occur at south-facing slopes (Romatschke et al., 2010).

Figure 3. South-facing treeline with *Pinus wallichiana* and *Juniperus indica* at ca. 4100 m, Manang, Nepal (Schickhoff, 21 September 2013).

On regional and local scales the climate of the Himalaya is distinctly modified by the vast topography. While the climate of the lowlands and foothills is characterized by warm conditions throughout the year, the very high elevations stand out due to extremely cold conditions, with temperatures below 0°C even during summer season. The distinct topographic characteristics lead to varying solar insolation rates and the development of autochthonous local-scale circulation systems, resulting in a rather complex near-surface temperature distribution. The local-scale distribution of precipitation rates is mainly influenced by wind- and leeward positions and again by topographically induced local-scale circulation patterns (Gerlitz, 2014).

Many studies show that high-mountain regions are particularly sensitive to climatic changes (e.g. Kohler et al., 2010). The enhanced radiative forcing due to anthropogenic greenhouse gas emissions and the albedo feedback due to shrinking glaciers and reduced snow cover rates during winter and spring result in an accelerated response to recent global warming. Observations show that temperature trends over the Himalaya by far exceed the global mean trend of 0.74°C during the previous century. For high elevations, temperature trends between 0.6 and 1°C per decade were detected (Shrestha et al., 1999; Liu and Chen, 2000). Based on elevation- and bias-adjusted ERA-Interim reanalysis data, Gerlitz et al. (2014) analysed spatial high-resolution temperature trends over the Himalaya for the period since 1989. During winter season, high temperature trends of up to +0.8°C per decade were detected over the eastern Himalaya. In pre-monsoon season, high temperature trends were found for the entire Himalayan Arc. Estimated temperature trends show a clear elevational gradient with maximum values of up to 1°C per decade at higher altitudes (Fig. 4). During monsoon season, temperature trends were found to be reduced throughout the target area. High temperature trends during post-monsoon season were detected only over the eastern Indus–Ganges lowlands. The study further indicates a decrease in frost days (up to -17 days per decade) in the Nepal Himalaya at elevations between 3000 and 3500 m. A significant positive trend of growing degree days was detected for the southern slopes of the Himalaya at elevations between 2000 and 3500 m (see Fig. 4).

Based on rain gauge observations, negative trends of annual precipitation (up to 20 % for the previous century) over the western Himalaya were identified by Duan et al. (2006), Bhutiyani et al. (2010), and Jain et al. (2013). This trend mainly results from decreasing summer precipitation rates after the 1960s, and is associated with a weakening of the Southern Oscillation and a decrease in temperature gradients over southern Asia due to high warming rates over the Indian Ocean during recent decades (Basistha et al., 2009; Naidu et al., 2009). Long-term trends of winter precipitation rates are slightly negative but not statistically significant (Bhutiyani et al., 2010). An enhanced frequency of winter and premonsoon drought events was reported for western Nepal by Wang et al. (2013). No statistically significant trends of annual precipitation rates could be detected for the eastern Himalaya (Jain et al., 2013). In combination with rising temperatures and accompanying increase in evapotranspiration rates, the decrease in precipitation over the Himalaya very likely leads to enhanced drought stress, particularly in the pre-monsoon season. Thus, recent climatic changes will inevitably affect growth patterns and seedling performance at Himalayan treelines, albeit to a regionally differentiated extent.

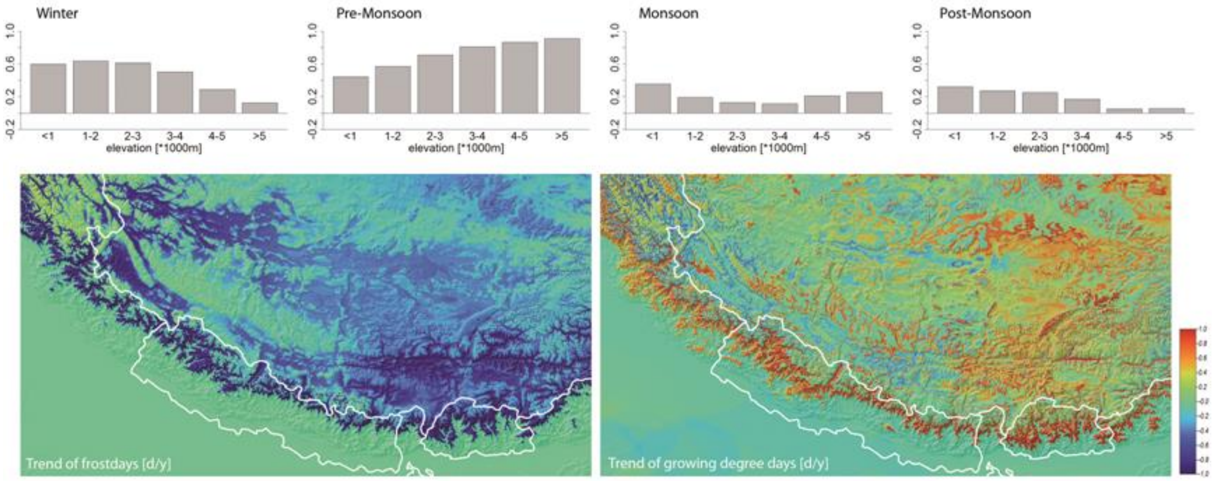

Figure 4. Seasonal temperature trends (°C per decade) for different elevational belts (top panels) and spatial distribution of trends for frost and growing degree days over the Himalaya (bottom panels) (according to Gerlitz et al., 2014).

4 Assessing sensitivity of Himalayan treelines

4.1 Susceptibility of treeline types and treeline forms

The occurrence of certain treeline types and treeline forms in a mountainous region indicates to some extent the susceptibility to respond to changing climatic conditions. Treeline types (climatic, orographic/edaphic, anthropogenic) are distinguished in this paper according to the environmental factors which control their altitudinal position (cf. Holtmeier and Broll, 2005). Climatic treelines are caused mainly by heat deficiency and, in extratropical regions, the duration of the growing season. It is the common alpine treeline type in zonal habitats under natural undisturbed conditions. By contrast, orographic treelines are always located below the climatically caused altitudinal limit, and are prevented from reaching their potential upper limit by factors such as steep topography, rock walls, talus cones, slope debris, or avalanche chutes. Edaphic treelines are often difficult to distinguish from orographic treelines, in particular when the steepness of slopes or the substrate on precipitous slopes prevents the accumulation of sufficient fine material and pedogenesis. On volcanic substrates, a lack of soil moisture may also prevent the treelines from reaching their upper climatic limit (Gieger and Leuschner, 2004). Anthropogenic treelines have been lowered from their natural position, often by several hundred metres, through a variety of human uses such as pastoral use, fire clearing, logging, collecting firewood, charcoal production, mining, and salt works. They are particularly common in long-settled mountain regions in Europe and Asia, where the average treeline depression is 150–300 m (Holtmeier, 2009).

The predisposition to respond to recent climate change varies considerably among the different treeline types. Climatic treelines show a comparatively high susceptibility and are more likely to reflect climate tracking since increases in temperature sums and growing season length will be inevitably reflected by growth patterns, regeneration, and treeline position, at least in the long-term (Holtmeier and Broll, 2007; Körner, 2012a). However, the direct influence of climate warming is variegated in complex ways by local-scale abiotic and biotic site factors and their manifold interactions that act as thermal modifiers. For instance, broad-scale climatic inputs are mediated at local scales by the varying microtopography in treeline ecotones and will exert a modified influence on soil temperatures, soil moisture, or the distribution of trees (Holtmeier and Broll, 2005, 2012; Case and Duncan, 2014). Thus, the sensitivity of climatic treelines varies with a considerable scope in the medium term (several years to a few decades). The long-term response in terms of treeline shifts might be more homogeneous, but the treelineposition will adjust to present climatic conditions only after a time lag of several decades to hundreds of years.

Unlike climatic treelines, orographic treelines are resistant to the effects of climate warming. As long as orographic factors such as debris slides, rockfalls, and snow avalanches prevent the establishment of trees, the fragmented spatial pattern of orographic treelines will not change significantly. Edaphic treelines will become more sensitive to a warming climate once pedogenetic processes accelerate and favour the establishment of tree seedlings and tree invasion. Anthropogenic treelines show considerable dynamics in recent decades with prolific regeneration, increased tree establishment within the treeline ecotone, and invasion into treeless areas above the anthropogenic forest limit. These directional changes are readily attributed to effects of global warming; they result, however, in most cases from the cessation of pastoral use or other human impact (Holtmeier, 2009; Schickhoff, 2011). It is imperative to disentangle the effects of decreasing land use and climate warming (cf. Gehrig-Fasel et al., 2007; Vittoz et al., 2008) in order to assess the potential for treeline advance beyond the current climatically determined upper limit. Nevertheless, anthropogenic treelines do not basically differ from climatic treelines in terms of sensitivity to climate warming, the potential effects of which, however, may be reduced due to radically altered site conditions and other after-effects of historical forest removal (Holtmeier and Broll, 2005).

The various treeline types occur in different frequencies in the vast Himalayan mountain system. According to our extensive field experience along the entire mountain arc, we estimate 85–90 % of treelines to be anthropogenic (Fig. 5), and only 10–15 % to be orographic/edaphic and climatically determined. Human occupation in many subregions began between hundreds (in some valleys) and thousands of years ago, and animal husbandry, timber logging, fuelwood collection, and the likes have long been integral parts of village economies. Thus, treeline ecotones have been transformed to a locally and regionally varying extent, and present landscape patterns at treeline elevations are cultural landscape patterns. Overgrazing and fire have been the main agents for lowering treelines (Beug and Miehe, 1999). Treelines at north- and south-facing slopes reflect contrasting utilization intensity.

As land use pressure is unevenly higher at south-facing slopes (in particular with regard to pastoral use), downslope extension of alpine pastures, depression of treelines, and even complete removal of forest cover are widespread phenomena at southern aspects throughout the mountain system (Miehe and Miehe, 2000; Schickhoff, 2005). Treeline depressions may be up to 500–1000 m (Miehe, 1997), in particular in localities where extensive alpine grazing grounds are not available. Treelines on south slopes are thus almost exclusively anthropogenic.

Figure 5. Anthropogenic treeline in Manang, Nepal, showing an abrupt transition to alpine grazing lands (Schickhoff, 24 September 2013).

North-facing slopes have a lower utilization potential for pastoral use. Nevertheless, a considerable depression of alpine treelines can be observed on shaded slopes as well, resulting from the extension of alpine grazing grounds and the over-utilization of subalpine forests (Schmidt-Vogt, 1990; Schickhoff, 2002). A representative example for the western Himalaya is Kaghan Valley, Pakistan, where the birch belt has been largely decimated, and uppermost coniferous forests depleted, resulting in a difference between current and potential treeline of up to 300m (Schickhoff, 1995). In most Himalayan regions we still witness a growing importance of the primary sector with land use intensification by local mountain farmers as a consequence of internally (population growth) and externally (lowland markets) generated pressure. Cessation of land use and subsequent landscape change in treeline ecotones has been observed to date only to a limited extent. Respective changes are largely confined to protected areas such as national parks and biosphere reserves. The percentage of anthropogenic treelines on north-facing slopes is lower than on south-facing slopes, i.e. some nearnatural treeline ecotones, more or less undisturbed by human impact, still persist on northern aspects in remote valleys which are sparsely populated, not connected to the road network, and/or where plants and animals are protected for religious reasons. These climatic treelines have to be considered unique research opportunities for detecting a clear climate change signal as a driver for treeline dynamics. Examples include treeline ecotones in the Black Mountains of Bhutan (Miehe and Miehe, 2000), in the Sygera Mountains in SE Tibet (Liang et al., 2011), and in the Rolwaling Valley in Nepal (Fig. 6). The latter is the location of a new treeline research programme from which first data are presented below. Due to the widespread steep and rugged terrain in the Himalaya, orographic/edaphic treelines are not uncommon but make up only a small percentage of all treelines. To summarize, the proportional distribution of treeline types in the Himalaya suggests that sensitivity and response to climate warming must be assessed cautiously. The vast majority are anthropogenic treelines, which, in addition, will be subjected to continued intensive land use in the foreseeable future. Thus, a substantial medium-term response is to be expected from the tiny fraction of climatic treelines only, and from those anthropogenic treelines, which are no longer exposed to important human disturbance.

Recently, Harsch and Bader (2011) discussed how treeline spatial patterns (treeline forms) are controlled by different mechanisms (at the levels of direct tree performance, causative stresses, and modifying neighbour interactions), and how the varying dominance of these controlling mechanisms modulate climate change responses of different treeline forms. They distinguished four primary treeline forms with a wide geographic distribution: (i) diffuse, with a gradual decrease in tree height and density along the treeline ecotone; (ii) abrupt, with forest stands directly bordering low alpine vegetation; (iii) island, with clumped patches or linear strips of krummholz or trees above closed forests; and (iv) krummholz, with a dispersed or contiguous belt of severely stunted or deformed trees above the upright forest. Applying this framework to alpine treelines globally, Harsch and Bader (2011) found diffuse treelines, formed and maintained primarily by growth limitation, to exhibit an earlier, stronger response signal, whereas abrupt, island, and krummholz treelines, controlled by seedling mortality and dieback, are comparatively unresponsive. They confirmed the link between treeline form and dynamics established earlier (Lloyd, 2005; Harsch et al., 2009) and supported the general suitability of treeline form for explaining the variability of response to climate warming.

Figure 6. Climatic treeline (3900–4000 m) on a north-facing slope in Rolwaling, Nepal (Schwab, 18 September 2014).

Although the present understanding of treeline pattern-process relationships is not sufficiently advanced to use treeline form to predict dynamics, and although land use effects on treelines are not explicitly addressed in Harsch and Bader’s approach, transferring their conclusions to Himalayan treelines (not included in their data set of 195 treeline sites with one or two exceptions) may give an additional indication of sensitivity and response. As indicated above, treeline forms in the Himalaya are predominantly controlled by anthropogenic disturbances, and cannot easily be classified into discrete classes. However, according to our field experience the occurrence of abrupt and island treelines under natural conditions can be virtually excluded. Abrupt treelines do occur (e.g. *Betula* treelines in Manang Valley, Nepal), but they are caused by land use (Shrestha et al., 2007). The vast majority of less disturbed or near-natural Himalayan treelines, mainly confined to north-facing slopes, should be categorized as krummholz treelines (cf. Sect. 2). Diffuse treelines are largely limited to less disturbed or nearnatural sites in southern aspects, which have become very rare. As treeline advances have been less commonly observed in krummholz treelines (Harsch and Bader, 2011), and responsive diffuse treelines are rare, near-natural Himalayan treelines will not considerably respond to climate warming, at least in terms of treeline shifts. In addition, nearnatural Himalayan krummholz treelines give way at their upper limit to a very dense alpine dwarf scrub heath so that tree seedlings are subjected to a strong competition. Nevertheless, increased vertical stem growth and enhanced recruitment of seedlings have been reported from many krummholz treelines worldwide (cf. Lescop-Sinclair and Payette, 1995; Harsch et al., 2009), presumably more related to a change in snow and winter climate conditions, and can also be expected at Himalayan treelines.

4.2 Seed-based regeneration

Any upward elevational shift of alpine treelines depends on the establishment of seedlings and their performance during early life stages (Germino et al., 2002; Holtmeier, 2009; Smith et al., 2009; Zurbriggen et al., 2013). Hence, as an indicator of treeline sensitivity, successful regeneration is considered to have higher significance than morphological or physiological responses of mature trees (Holtmeier and Broll, 2005). When interpreting tree recruitment as evidence of response to recent environmental change, however, site, climate, and species-specific regeneration cycles have to be taken into account and should be backed by robust causeand- effect analysis (Körner, 2012a). To understand underlying mechanisms of treeline dynamics, a multitude of environmental factors and processes controlling seed-based regeneration have to be included in respective analyses and correlated with seedling establishment, survival, and growth. In recent years, an increasing number of studies have investigated the response of treeline seedlings to changing environmental factors such as soil temperature, soil moisture, soil nutrients, light conditions, herbivory, and competition /

facilitation (e.g. Maher and Germino, 2006; Anschlag et al., 2008; Batllori et al., 2009; Hofgaard et al., 2009; Kabeya, 2010; Munier et al., 2010); some studies have also explicitly addressed the relative importance of multiple factors (Barbeito et al., 2012; Zurbriggen et al., 2013).

In the Himalaya, only very few studies on treeline seedlings have been conducted so far, and tree recruitment in treeline ecotones is not well understood (Schickhoff, 2005; Dutta et al., 2014). However, some preliminary evidence with regard to using regeneration as an indicator of treeline sensitivity can be inferred. The majority of studies on seedbased regeneration have been carried out in Nepal. Shrestha et al. (2007) found *Betula utilis* treeline forests in Manang Valley, Annapurna Conservation Area, sufficiently generating with a reverse J-shaped diameter distribution. Along vertical transects, *Betula* seedlings and saplings were common up to an altitudinal distance of 50 m above the treeline. Seedlings could not, however, establish under their own canopy when tree density and basal area exceeded certain threshold values. Canopy cover (light) and soil moisture largely determined reproductive success. Seedlings of *Abies spectabilis* were abundant up to 3900 m but absent above 4000 m. Continuous regeneration as indicated by reverse J-shaped density–diameter curves and high densities of seedlings and saplings was also assessed in other studies in treeline forests in Manang, focusing on *Abies spectabilis* (Ghimire and Lekhak, 2007) and *Pinus wallichiana* (Ghimire et al., 2010). *Abies* seedling abundance was positively correlated with soil moisture and nutrients (phosphorus), whereas altitude was the only significant predictor of *Pinus* seedling density. Shrestha (2013) also observed continuous tree recruitment of Pinus *wallichiana* in Ngawal/Manang (southfacing slope) and *Abies spectabilis* in Lauribinayak/Langtang National Park (north-facing slope), with seedlings occurring up to 60 m above current treelines in 4120 m/3910 m. Corresponding results were obtained by Gaire et al. (2011) at treelines in southern Langtang National Park, who found high levels of recruitment of *Abies spectabilis* in recent decades, with seedlings and saplings at much higher elevations than uppermost cone-bearing tree individuals. Recent detailed observations in Manaslu Conservation Area (Gaire et al., 2014) indicate a considerable upward shift and excellent recruitment of *Abies spectabilis*, positively correlated with monthly maximum temperature in most of the months of the current year and with May–August precipitation. Another study on treeline fir (*Abies spectabilis*) recruitment in Mt. Everest Nature Reserve (S Tibet) achieved consistent results, with significant tree recruitment in the recent three decades that showed a positive correlation with mean summer air temperature (Lv and Zhang, 2012).

Detailed information on treeline seed-produced regeneration from other Himalayan subregions is scarce. In the vast Indian Himalaya, some knowledge has been accumulated on regeneration dynamics in lower altitude forests (e.g. Singh and Singh, 1992), but only very scanty information from treeline ecotones has been published. Treeline ecotones in Kumaon/Uttarakhand (Pindar, Sarju, and Ramganga catchments), heavily influenced by grazing and browsing, showed a low seedling/sapling density of *Abies pindrow* but a much better regeneration status of *Betula utilis* and *Rhododendron campanulatum* (Rawal and Pangtey, 1994). Gairola et al. (2008) reported intense regeneration from less disturbed upper subalpine forests in Garhwal/Uttarakhand. Dubey et al. (2003) observed increasing establishment of pine saplings (*Pinus wallichiana*) above the treeline zone in Parabati Valley, Himachal Pradesh, India, and ascribed the recruitment pattern to climate warming. Intense regeneration of *Betula utilis* at treelines in Uttarakhand and Himachal Pradesh and invasion of alpine meadows by birch seedlings was highlighted in a recent study by Rai et al. (2013). Information on regeneration at treelines from the Hindu Kush, Karakoram, and W Himalayan ranges of Pakistan is even more meagre. A comprehensive study of high-altitude forests including upper subalpine forest stands in the Karakoram (Schickhoff, 2000) revealed retarded growth processes and slow stand development cycles with generally low regeneration rates, associated with low site productivity rather than grazing impact.

Research on treeline seedlings performance in the eastern Himalaya is in its infancy as well. Some detailed studies on *Abies densa* regeneration and its controlling factors near alpine treelines in Bhutan showed intense recruitment (Gratzer et al., 2002; Gratzer and Rai, 2004). Expanding treeline populations of Smith fir (*Abies georgei* var. *smithii*) and infilling of treeline ecotones with intense, microsite-dependent clumping of abundant seedlings were reported from the Sygera Mountains (SE Tibet) (Ren et al., 2007; Wang et al., 2012), in accordance with observations from Liang et al. (2011), who assessed considerably increased

Smith fir recruitment in recent decades, significantly positively correlated with both summer and winter temperatures. First experimental studies (transplant experiment) in an adjacent study area indicated early-season freezing events to be the major limiting factor determining mortality of fir seedlings above the current treeline (Shen et al., 2014). High rates of regeneration with the percentage of seedlings/saplings increasing upslope across the treeline ecotone were assessed in the Hengduan Mountains (NW Yunnan) by Wong et al. (2010).

First results from ongoing research projects of the present authors in two study areas in Nepal (Rolwaling Valley, Gaurishankar Conservation Area; Langtang Valley, Langtang National Park) corroborate the emerging pattern of a generally intense regeneration at Himalayan treeline sites, as long as pastoral use is not the major force determining seedling performance.

The alpine treeline in Rolwaling Valley, located in east-central Nepal (27°520’N, 86°250’E) and virtually undisturbed by human impact, corresponds to the krummholz treeline form (north-facing slope). Upper subalpine forests are primarily composed of *Betula utilis* and *Abies spectabilis*, with *Rhododendron campanulatum* and *Sorbus microphylla* forming a second tree layer. Closed forests give way to an extensive krummholz belt of *Rh. campanulatum* at 3900 m (NW-exposed)/4000 m (NE-exposed), which turn into alpine *Rhododendron* dwarf scrub heaths at ca. 4000 m/4100 m. We analysed seedling density on NW and NE slopes in upper Rolwaling across the treeline ecotone, divided into four altitudinal zones (Table 1).

Within each zone, 12 plots (20 m x 20 m) were randomly selected. We assessed largely prolific regeneration with seedling establishment of *Betula*, *Abies* and *Sorbus* to some extent far above the upper limit of adult trees (Fig. 7).

Some individuals of more than 2 m height even grow vigorously above the krummholz belt: a small birch tree of 2.4 m height was found in 4140 m. Maximum seedling/sapling density occurs in elevational zone B (more than 9000 N ha^{-1}), where *Rh. campanulatum* has its most intense recruitment (see Table 1). Young growth density sharply decreases towards the alpine tundra, in particular with *Abies* and *Betula*, which also show considerably higher seedling/sapling abundance on the NW slope. The average elevation above sea level of maximum seedling/sapling density is distinctly higher on the NE slope (Fig. 8), which experiences higher sunshine duration and heat sum. *Rhododendron* and *Sorbus* seedlings/saplings are distributed along the entire treeline ecotone. We found a negative correlation between abundance and density of *Rh. campanulatum* and recruitment of other tree species (unpublished data), the seedling establishment of which is obviously impeded by the permanently dense foliation of evergreen *Rhododendron* and by potential allelopathic effects that have been shown for other species of this genus (Chou et al., 2010). Thus, the dense krummholz belt appears to be an effective barrier for upslope migration of other tree species. Reproductive success was also found to be generally positively correlated with a finely structured microtopography.

Tab. 1: Number of seedlings/saplings (< 7 cm breast height diameter; N ha^{-1}) of *Betula utilis*, *Abies spectabilis*, *Rhododendron campanulatum*, and *Sorbus microphylla* according to slope aspect and altitudinal zone.

	Altitudinal zone	Altitude (m)	*Betula utilis*	*Abies spectabilis*	*Rhododendron campanulatum*	*Sorbus microphylla*	Total
NE slope	A	3780-3880	754	100	517	1346	2717
	B	3920-3980	1081	1067	7854	233	9262
	C	4020-4080	13	0	5908	500	6421
	D	4120-4220	0	0	379	21	400
Total			875	1167	14 658	2100	18 800
NW slope	A	3760-3780	3788	3488	1129	1133	9538
	B	3820-3880	1067	613	6675	679	9034
	C	3920-3980	58	58	4075	275	4466
	D	4020-4240	8	13	1475	71	1567
Total			4921	4172	13 354	2158	24 605

Figure 7. *Abies spectabilis* sapling at 4200 m in *Rhododendron anthopogon* dwarf scrub heath, Rolwaling, Nepal, ca. 200 m above treeline (Schickhoff, 20 August 2013).

A first evaluation of the importance of soil temperature and soil moisture for seedling/sapling density of *Abies*, *Betula*, *Rhododendron,* and *Sorbus* has been conducted on the basis of 32 plots, on which these variables were recorded in 10 cm soil depth from May 2013 to April 2014 (Fig. 9). The results show significantly positive correlations of seedling/sapling abundance with soil moisture for *Abies*, *Betula*, and *Rhododendron*, and with soil temperature for *Abies*, *Betula*, and *Sorbus*, in each case over almost all size classes. Thus, higher soil moisture and soil temperatures indicate higher recruitment density of the majority of treeline tree species. A negative correlation with soil moisture was merely assessed for germinants and small saplings of *Sorbus microphylla*, in contrast to larger recruits of this species. *Rh. campanulatum* saplings (up to a height of 2 m) were found to be negatively correlated with soil temperature, germinants, and large shrubs, but showed a positive correlation (see Fig. 9). Total soil moisture values did not differ much between NE and NW slopes.

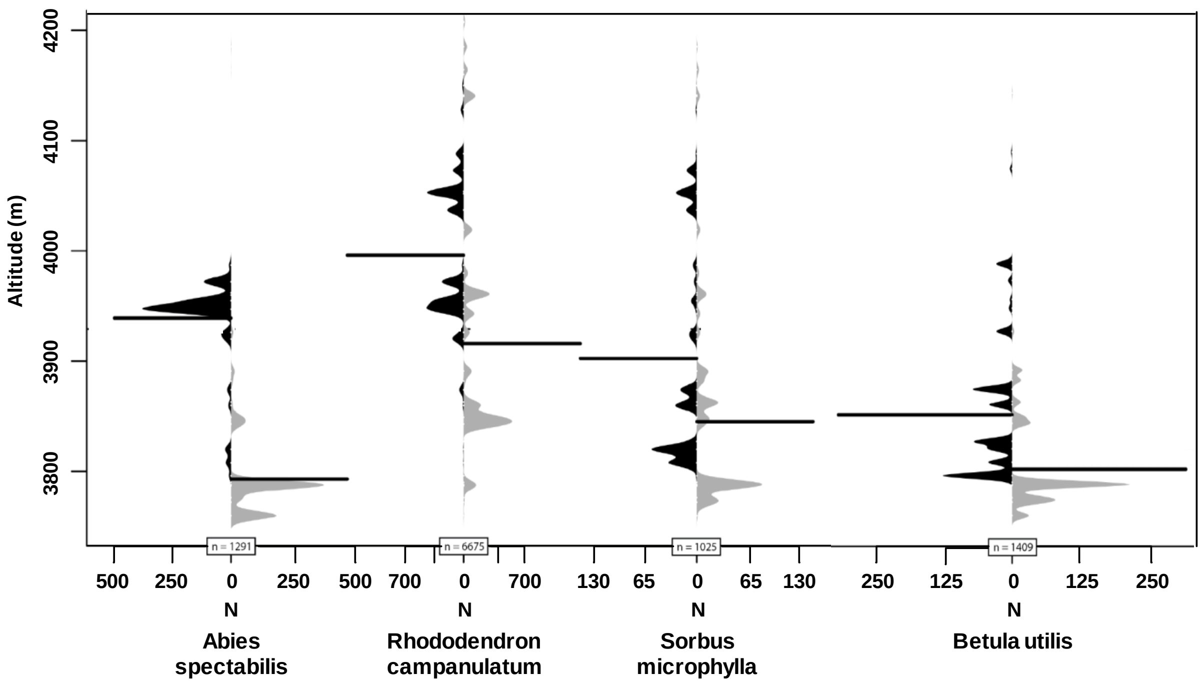

Figure 8. Seedling/sapling density of treeline tree species in the treeline ecotone in Rolwaling Valley according to altitude and slope exposure (black: NE slope; grey: NW slope).

The treeline physiognomy and vegetation zonation of the study sites in Langtang Valley, ca. 100 km to the west, is more or less in accordance with that of Rolwaling. The *Rh. campanulatum* krummholz belt, however, is not as dense and often disintegrated, so that uppermost birch forest stands are occasionally adjoining *Rhododendron* dwarf scrub heaths that may have invaded downslope into former krummholz sites. Langtang treeline ecotones and its vegetation patterns, though near-natural, have been and still are affected to a much larger extent by pastoral and forest use compared to those in Rolwaling. We studied regeneration dynamics on 70 plots along elevational transects across the treeline ecotone with a stratified random sampling. In accordance with the observations in Rolwaling, the production of viable seeds and the supply of treeline ecotones with fertile seeds are obviously sufficient to generate relatively high rates of seedling establishment, even beyond the actual upper limit of contiguous forests between 4000 and 4100 m. Maximum seedling/sapling density occurs at 3900 m (10 665 ha^{-1}) and 3950 m (10 075 N ha^{-1}), before the recruit abundance sharply decreases above 4100 m, slightly above the transition from cloud forests to dwarf scrub heaths (Table 2).

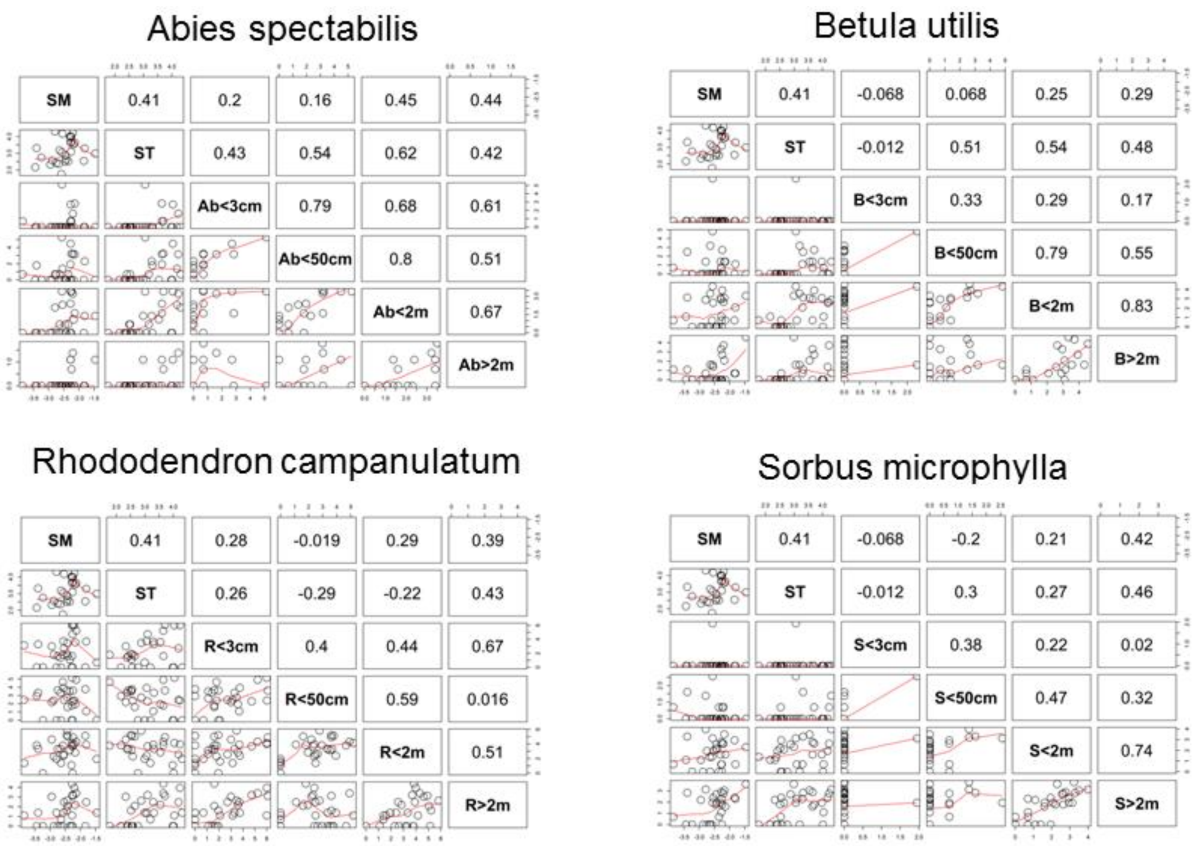

Figure 9. Spearman rank correlations between seedling/sapling abundance and soil temperature and soil moisture in the treeline ecotone in Rolwaling Valley.

The vast majority of all seedlings/saplings are *Sorbus microphylla* (54 %) and *Rh. campanulatum* individuals (40 %); these occupy in particular the size class 0–19 cm (98 %) (Fig. 10). In contrast, recruitment of *Abies spectabilis* is relatively sparse, and obviously related to grazing impact and the removal of adult trees as seed sources. Regeneration of *Betula utilis* is also less intense. However, *Betula* seedlings/saplings are far more homogeneously distributed across the size classes compared to the other species (see Fig. 10). Numerous saplings of greater size classes became established at the treeline and above the upper limit of contiguous forests (Fig. 11). The uppermost *Betula* tree individual was found at 4215 m, ca. 150 m above the current treeline, with a height of 4.5 m and a breast height diameter of 14.5 cm. In summary, seed-based regeneration within and beyond treeline ecotones of Rolwaling and Langtang valleys does not appear to restrict these treelines from being prone to responding to climate warming.

Table 2. Cumulative numbers of seedlings/saplings (N ha^{-1}) of *Betula utilis, Abies spectabilis, Rhododendron campanulatum*, and *Sorbus microphylla* in the treeline ecotone in Langtang Valley according to altitude and size classes (dbh: diameter at breast height).

	Size class (cm)									
Altitude (m)	0-19	20-49	50-99	100-149	150-199	200-299	300-399	400-499	500-7 cm dbh	Total
3850	5441	1134	522	631	603	131	69	69	78	8678
3900	6269	1834	909	628	719	172	59	41	34	10 665
3950	6778	1225	566	500	434	122	75	169	206	10 075
4000	4741	772	513	459	425	63	34	84	159	7250
4050	3694	403	231	213	253	97	75	78	75	5119
4100	3631	497	253	269	259	113	69	34	25	5150
4150	397	184	69	47	75	31	22	16	19	860
4200	19	28	16	13	9	3	0	0	0	88
Total	30 970	6077	3079	2760	2777	732	491	491	596	47 885

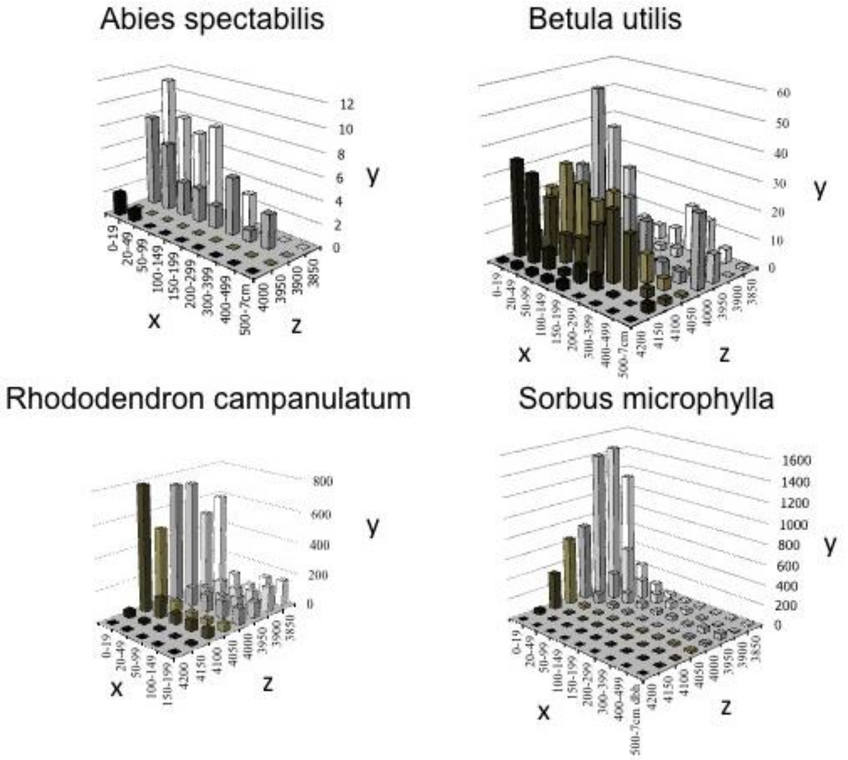

Figure 10. Seedling/sapling density in the treeline ecotone in Langtang Valley according to altitude and size classes (x axis: size class; y axis: quantity; z axis: altitude).

4.3 Tree physiognomy and growth patterns

Climatic changes affect tree physiognomy at treelines since height growth of trees is very sensitive to decreasing temperatures with increasing altitude, resulting in climatically shaped growth forms that trees in this harsh environment usually display (Holtmeier, 2009; Körner, 2012a). Varied other abiotic and biotic site factors such as wind, snow, nutrient supply, and browsing also influence the development of growth forms at treelines, but tree physiognomy at least partly reflects changing environmental conditions related to climatic warming. The phenotypical response does not necessarily mirror long-term climatic trends: a few favourable years with undisturbed growth can be sufficient to trigger a change in physiognomy (Holtmeier and Broll, 2005). On the other hand, deteriorating climatic conditions or extreme climatic events may lead to physiognomic changes caused by dieback. While several studies have reported accelerated height growth of previously low-growing tree individuals from different treeline ecotones (e.g. Lescop-Sinclair and Payette, 1995; Kullman, 2000; Kullman and Öberg, 2009), no such information from Himalayan treelines is available to date. However, it can be inferred from remote-sensing-based studies that the expansion of treeline ecotones, subalpine forests, and alpine scrub in recent decades is accompanied by enhanced height growth of individual trees. Rai et al. (2013) detected a substantial increase in fir and birch treeline forests in Himachal Pradesh and Uttarakhand during 1980–2010 that most likely has included positive changes in the physiognomy of single trees. Respective data from ongoing studies in Rolwaling are currently being evaluated.

Figure 11. Tall saplings of *Betula utilis* (ca. 2 m) growing 100–150m above the current treeline in Langtang, Nepal (Schickhoff, 21 July 2010).

Better evidence can be ascertained for growth responses in the Himalaya in terms of diameter growth. Generally, radial growth is less affected than height growth by decreasing temperatures when approaching the upper treeline but shows a much more pronounced response to climate warming (Körner, 2012a). It has been shown for *Pinus cembra* and *Picea abies* in the European Alps that the declining trend in tree radial growth toward the treeline that prevailed in the nineteenth century has disappeared in the twentieth century due to rising temperatures, and that mature trees at treeline currently grow as fast as trees in the upper montane forest (Paulsen et al., 2000). Other comparable growth enhancements at treelines have been assessed, for example, for *Picea*, *Pinus*, and *Larix* in the Italian Alps (Rolland et al., 1998); *Pinus longaeva* in western North America (Salzer et al., 2009); *Nothofagus pumilio* in southern Argentina (Villalba et al., 1997); *Picea schrenkiana* in the Tianshan Mountains (Qi et al., 2015); and *Betula ermanii* in Kamchatka (Dolezal et al., 2014). Growth responses to a warming climate, however, tend to be different where a lack of available moisture becomes a controlling factor, e.g. in arid or semiarid regions or in regions with seasonal drought periods. Drought stress as a local factor impeding tree growth in recent decades has been supposed for different treeline environments (e.g. Lloyd and Fastie, 2002; Daniels and Veblen, 2004; Dulamsuren et al., 2010; Zhang et al., 2011; Fajardo and McIntire, 2012; Ohse et al., 2012).

In the Himalaya, only very few dendroclimatic studies have been conducted at treeline elevations. However, there is increasing evidence suggesting that growth response of treeline trees to climate change and variability is spatiotemporally differentiated, species-specific, and not unidirectional. In general, tree-ring growth in the E Himalaya is less sensitive to climate variation compared toW Himalayan sites and trees (Bhattacharyya and Shah, 2009), and most studies reported radial growth of treeline conifers to be more responsive to temperature than precipitation change, with western and central Himalayan conifers being more responsive to winter and pre-monsoon temperatures and E Himalayan conifers often being more responsive to summer temperatures.

Some studies reported consistent responses of tree growth to recent climate warming. Tree-ring-width chronologies of *Pinus wallichiana*, *Cedrus deodara*, and *Picea smithiana* from high-altitude forests and treeline sites in Kinnaur (Himachal Pradesh) and Gangotri (Uttarakhand) have showed an unprecedented growth enhancement during recent decades and a strong positive relationship to the mean annual and winter (DJF) temperatures; the anomalously higher growth was thus ascribed to the overall warming trend over the region (Singh and Yadav, 2000; Borgaonkar et al., 2009, 2011). Ring width chronologies of *Abies georgei* var. *smithii* growing at treeline in the Sygera Mountains (SE Tibet) revealed accelerated growth in the past decades and significantly positive correlations with monthly mean and minimum temper- atures of most months, particularly in summer (Liang et al., 2009, 2010). However, the significant extension of the growing season at the same treeline by ca. 21 days during the past 50 years has not directly affected the radial growth of Smith fir to date (Liu et al., 2013). Zhu et al. (2011) reported a similar response to summer temperatures for *Picea likiangensis* var. *balfouriana* at adjacent treelines.

Recent accelerated growth has not been confirmed in the Karakoram Mountains, but it has been established for neartreeline sampling locations of *Juniperus turkestanica*, *Pinus* *wallichiana*, and *Picea smithiana* that temperature variation predominantly limits tree growth (Esper et al., 2002, 2007). High-elevation junipers in semiarid Lahul (Himachal Pradesh) are obviously more responsive to precipitation during winter and spring months (Yadav et al., 2006; see also Yadav et al., 2011). Gaire et al. (2014) found tree growth of *Abies spectabilis* in Manaslu Conservation Area (Nepal) to be positively correlated with higher winter temperatures prior to growing season, and stressed the positive effects of earlier snow melt and increased melt water supply for growth. Similarly, Bräuning (2004) reported a strong positive relationship between *Abies spectabilis* ring width and November–January temperature in Dolpo (W Nepal). The ring width of several treeline conifers in SE Tibet and NW Yunnan was also found to be sensitive to winter season temperature, while their maximum latewood density was positively correlated with summer temperature (Bräuning and Mantwill, 2004; Bräuning, 2006; Bräuning and Grießinger, 2006; Fan et al., 2009). Warmer conditions during winter season facilitate the storage of higher levels of hydrocarbonates and are beneficial to root system activity and carbon absorption and transportation (He et al., 2013). A positive relationship to winter temperatures was also ascertained for *Abies densa* near treelines in Sikkim and Arunachal Pradesh, while summer temperatures were inversely related to tree growth (Bhattacharyya and Chaudhary, 2003).

An increasing number of studies in the western and central Himalaya have revealed a strong sensitivity of tree growth to pre-monsoon temperature and humidity conditions. Yadav et al. (2004) analysed ring width chronologies of *Abies spectabilis* from four treeline sites in Himachal Pradesh and Uttarakhand and found significantly negative correlations with long-term pre-monsoon temperature series. These findings are in accordance with results from other high-elevation sites in Uttarakhand using *Taxus baccata* (now *Taxus wallichiana*) tree-ring sequences (Yadav and Singh, 2002) and *Cedrus deodara* tree-ring data (Bhattacharyya and Yadav, 1990), and also correspond to *Abies spectabilis* tree growth–climate relationships analysed near treeline in Humla District (Nepal) (Sano et al., 2005) and at the treeline ecotone in Langtang National Park (Nepal) (Gaire et al., 2011; Shrestha, 2013). Higher temperatures during the relatively dry spring months lead to increased evapotranspiration and to soil moisture deficits, impeding tree growth in particular on sites which are prone to drought stress. A negative correlation of pre-monsoon temperature with total ring width and a positive correlation of pre-monsoon precipitation with ring width are apparently widespread patterns in western and central Himalayan tree growth–climate relationships (cf. Borgaonkar et al., 1999; Pant et al., 2000; Cook et al., 2003; Ram and Borgaonkar, 2013) and have been used accordingly for temperature and precipitation reconstruction (e.g. Yadav et al., 1997, 1999; Singh and Yadav, 2005, 2014; Singh et al., 2006; Ram and Borgaonkar, 2014). A significant negative correlation with May temperature has also been detected for *Juniperus tibetica* on the semiarid southern Tibetan Plateau (He et al., 2013; Liu et al., 2013), a positive relationship, by contrast, for Larix griffithiana in humid Arunachal Pradesh (Chaudhary and Bhattacharyya, 2000).

Recently, the pre-monsoon period has been shown to be also critical for broad-leaved treeline trees. After the dendroclimatological potential of the Himalayan birch had been pointed out by Bräuning (2004), Bhattacharyya et al. (2006) reported in a preliminary study of tree-ring data of *Betula utilis*, growing near the snout of Gangotri Glacier (Uttarakhand), that higher temperatures and less rainfall during pre-monsoon months results in lower tree growth. Dawadi et al. (2013) corroborated this finding and assessed, for the growth of birch trees at treeline sampling sites in Langtang Valley (Nepal), a positive correlation with March–May precipitation and an inverse relationship with pre-monsoon temperatures. Reduced pre-monsoon moisture availability being a primary growth-limiting factor for *Betula utilis* at treeline and the coincidence of years with a high percentage of missing rings or narrow rings with dry and warm pre-monsoon seasons was once again confirmed by Liang et al. (2014) for study sites in Sagarmatha National Park, Langtang National Park, and Manaslu Conservation Area (Nepal) (for Manaslu see also Gaire et al., 2014). Recent research by the present authors investigated a ring width chronology of *Betula utilis* from treeline sites in Langtang Valley dating back to AD 1657 and found a negative correlation of treering width with pre-monsoon temperature and a positive correlation with pre-monsoon precipitation (Lange et al., unpublished data). Pre-monsoon climate definitely affects growth patterns of the Himalayan birch to a large extent, however, contrary to Liang et al. (2014, p. 16) we refrain from concluding that this species is increasingly at risk of survival, and from qualifying respective treelines as “drought-induced alpine timberlines” (op. cit., p. 2). Co-dominant conifer treeline species are more temperature-sensitive, and the altitudinal position of Himalayan birch treelines corresponds more or less to global characteristics of growing season length, thermal sums, and mean air and soil temperatures common at treelines induced by heat deficiency (cf. Körner, 2012a). As a pioneer species with relatively wide ecological amplitude, *Betula utilis* also thrives under distinctly drier conditions in the NW Himalaya and Karakoram, and has survived severe drought periods in the past (recently reconstructed by Cook et al., 2010).

5 Treeline shifts

As evident from repeated climatically caused treeline fluctuations during the Holocene, treeline shifts are to be expected in response to recent climate change. In most cases, however, the response will be a long-term response, of the order of several decades to a hundred or more years. Most likely, treeline positions are always lagging behind climatic fluctuations, and the global treelines we observe today are each in a specific state of climate tracking. Thus, the globally heterogeneous response patterns with advancing and stagnating or rather unresponsive treelines come as no surprise. For the Himalaya, stagnating treelines as well as treeline advances of partially significant dimension, mostly attributed to climate warming, have been reported to date. A major difficulty in evaluating currently available observations of treeline shifts in the literature is that they are not based on a comparable treeline concept. For example, the position of tree seedlings is often hastily taken to calculate treeline shifts without considering that simply the presence of seedlings is not synonymous with an actual treeline advance. Only the sustainable transition into subsequent sapling size classes would increase the potential of a treeline shift (cf. Graumlich et al., 2005). For the Himalaya, only very few studies on spatiotemporal treeline dynamics are available. Some are based on thorough dendroecological or forest-ecological fieldwork and have been conducted at near-natural treelines. For example, Liang et al. (2011) analysed Smith fir stands at the treeline in the Sygera Mountains (SE Tibet) and found the treeline position to have moved upslope only slightly and insignificantly, whereas the population density of trees and the number of seedlings have considerably increased after the 1950s. These findings are in line with recent research of the present authors on the treeline in Rolwaling Valley (Nepal) indicating increasing stand densities but no significant alteration in treeline position (unpublished data). Gaire et al. (2014) recently investigated upward shifting of tree species limits in the treeline ecotone at Kalchuman Lake (Manaslu, Nepal); they reported extraordinary migration rates of *Abies spectabilis* since AD1850 but that the upper distribution limit of *Betula utilis* has remained stagnant in the past decades. Migration rates were calculated on the basis of uppermost seedling position. However, given the generally low survival rate of seedlings in treeline ecotones during the first years after germination, and considering critical later life stages after projecting above the winter snow cover, it is rather unlikely that recorded upper species limits will be persistent ones. A more or less stationary treeline position over recent decades in two study sites in Nepal (Manang, Langtang National Park) was assessed by Gaire et al. (2011) and Shrestha (2013).

Other studies on treeline shifts are based on remote sensing. Bharti et al. (2012) used Landsat imagery and found an overall increase in the green biomass of treeline ecotone in Nanda Devi Biosphere Reserve (Uttarakhand) during 1980-2010, in particular of the subalpine forest's canopy, but no shift of the upper treeline. In contrast, two other studies in the same area reported globally exceptional and unprecedented treeline advances of more than 300 m in recent decades (Panigrahy et al., 2010; Singh et al., 2012); these results, however, have been criticized as unreliable due to methodological shortcomings (cf. Bharti et al., 2011; Negi, 2012; Rawat, 2012). Another Landsat-based change detection study of the treeline ecotone in Himachal Pradesh and Uttarakhand indicated an expansion of fir and birch forests in recent decades (Rai et al., 2013). Based on repeat photography, Baker and Moseley (2007) documented a significant infilling of the tree limit ecocline and an upward shift of the timberline of almost 70 m in elevation at a slope in the Hengduan Mountains (NW Yunnan) since AD 1923, and they argued that climate warming contributed to the elevational advance of the alpine treeline. However, the expansions and shifts, when detected at anthropogenically depressed treelines, are rather an effect of the cessation of land use and other human disturbances than a result of climate change.

Recently, an increasing number of modelling approaches have been applied to gain a better understanding of treeline dynamics in response to climate and land use change and of underlying process–pattern relationships (e.g. Dullinger et al., 2004; Wallentin et al., 2008; Paulsen and Körner, 2014). In the Himalaya, neither modelling approaches to predict the response of individual treeline systems nor modelling studies to project future geographic distribution of treeline tree species have been conducted so far. Recently, initial modelling studies with regard to environmental niches of the genus *Rhododendron* in Sikkim and *Betula utilis* in Uttarakhand have been published (Kumar, 2012; Singh et al., 2013).

Ecological niche models have proven to be a valuable tool of linking the occurrence or abundance of a species to environmental and/or geographical variables, providing predictions of species distribution ranges or potential habitat suitability (e.g. Elith et al., 2010). They are usually calibrated based on current environmental conditions and extrapolated to future scenarios, based on the assumption of niche conservatism (Wiens et al., 2010). We used ecological niche modelling to forecast the range shift of *Betula utilis* under novel climate conditions in AD 2070 (Fig. 12). All models were calculated using the maximum entropy algorithm (Phillips et al., 2006), implemented in the software Maxent, version 3.3.3k. Presence-only occurrence data of *Betula utilis* were accessed via the Global Biodiversity Information Facility (gbif.org). The database hosted 193 georeferenced records (1970–2014) with non-known coordinate issues for the Himalayan region. Ninety-three records were added compiled from the present author's database. After filtering the occurrence points to reduce spatial autocorrelation, 173 records were used for model analysis. We used bioclimatic raster data and a digital elevation model (DEM) obtained from WorldClim (worldclim.org; Hijmans et al., 2005). For future climate scenario, 19 bioclimatic variables of MIROC5 rcp60 were used and projected to 2070 (downscaled IPCC5 (CMIP5) data; Hijmans et al., 2005). Spatial resolution of all grids was 30 arc seconds (1 km). We used a geographically structured approach with three bins; accordingly, occurrence data were split in 138 training data points and evaluated with the remaining 35 data points. Models were fitted and projected to both current and future climate using all features and different regularization parameters. Models were evaluated using the receiver operating characteristic (area under the curve, ROC, AUC).

Consistent with current scientific knowledge, the averaged models (AUC 0.922) mapped upslope distribution range shifts.

As a result of driving by significant bioclimatic variables such as mean diurnal range (monthly temperature: min–max), minimum temperature of coldest month, slope and annual precipitation, and mean temperature of wettest month, the potential habitat of *Betula utilis* is predicted to shift from lower to higher elevations and to expand into new habitats north of the Himalayan range (see Fig. 12). Significant upslope expansions are modelled for Transhimalayan ranges in S Tibet. Range contractions are forecasted for the lesser W Indian Himalaya, the S Hindu Kush, and the Wakhan Corridor. Gaining a better understanding of potential range shifts of alpine treeline species under climate change scenarios is supported by such model results, which also provide insights into decision makers in climate change mitigation and biodiversity conservation.

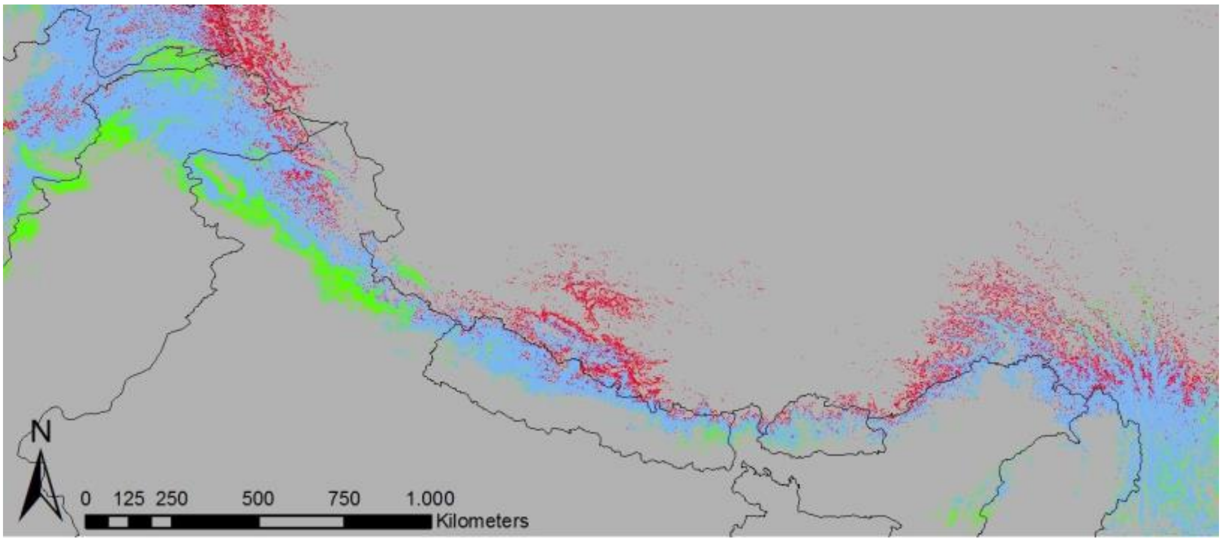

Figure 12. Potential range shift of *Betula utilis* under novel climate conditions in AD 2070, based on ecological niche modelling.

6 Conclusions

Treeline environments in the Himalaya are very heterogeneous, implying limitations for broad generalizations on treeline sensitivity and response to climate change. Nevertheless, several key conclusions emerge from the present study. Anthropogenic treelines are predominant in the Himalaya, i.e. expansions of treeline vegetation and treeline shifts at those treelines are related to declining land use intensity and should not be misunderstood as being primarily triggered by climate change. To distil the climate change signal with high temperature trends over the Himalayan arc, one has to investigate near-natural or less disturbed treelines, which have become very rare and largely confined to north-facing slopes, where they are usually developed as krummholz treelines. Strong competition within the krummholz belt and dense dwarf scrub heaths further upslope adversely affects upward migration of tree species and treeline shifts. This prevailing environmental setting suggests a relatively low responsiveness of near-natural Himalayan treelines and a significant movement in elevation only in the long term. On the other hand, the evaluation of seed-based regeneration showed that recruitment is usually intense, with huge seedling/sapling presence within and beyond the treeline ecotone. These results suggest a high proneness to respond and further suggest that a future treeline advance will be significantly controlled, once seeds have dispersed upslope and germinated, by the species-specific competitive abilities during the recruitment phase or the effectiveness of recruitment suppression in the krummholz and dwarf scrub belts. Tree growth–climate relationships, though species-specific, revealed a high sensitivity of mature treeline trees to temperature. Growth patterns in the western and central Himalaya are particularly responsive to pre-monsoon temperature and humidity conditions. The future pre-monsoon climate change may therefore be an important driver of physiological and morphological responses. Environmental niche modelling of *Betula utilis* indicates a probable range expansion in the coming decades, suggesting that the bioclimatic preconditions for a future treeline advance will be existent. Considering species-specific physiological responses and competitive traits, complex and nonlinear responses of individual Himalayan treeline systems to climate change can be anticipated. Treeline shifts are of substantial ecological relevance due to possible implications for regional biodiversity and ecological integrity. A widespread upward encroachment of subalpine forests would displace regionally unique alpine tundra habitats and possibly cause the loss of alpine species.

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Book chapter (published)

16. Treeline responsiveness to climate warming: Insights from a krummholz treeline in Rolwaling Himal, Nepal

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Abstract At a global scale, the elevational position of natural upper treelines is determined by low temperatures during growing season. Thus, climate warming is expected to induce treelines to advance to higher elevations. Empirical studies in diverse mountain ranges, however, give evidence of both advancing alpine treelines as well as rather insignificant responses. Himalayan treeline ecotones show considerable differences in altitudinal position as well as in physiognomy and species composition. To assess the sensitivity of a near-natural treeline to climate warming at local scale, we analysed the relations between changes of growth parameters and temperature gradients along the elevational gradient in the treeline ecotone in Rolwaling valley, Nepal, by a multispecies approach. We observed species-specific transition patterns (diameter at breast height, height, tree and recruit densities), and varying degrees of abruptness of these transitions across the treeline ecotone resulting in a complex stand structure. Soil temperatures are associated with physiognomic transitions, treeline position, and spatial regeneration patterns. In conclusion, treeline tree species have the potential to migrate upslope in future. Upslope migration, however, is controlled by a dense krummholz belt of *Rhododendron campanulatum*. Currently, the treeline is rather stable; however we found a prolific regeneration as well as signs of stand densification. Given the spatial heterogeneity of Himalayan treeline ecotones further studies are needed to fully understand the complex conditions for establishment and development of tree seedlings and the responsiveness of Himalayan treeline ecotones to climate change.

16.1 Introduction

At a global scale, the position of natural upper treelines is determined by low air and soil temperatures during growing season (e.g. Troll 1973; Stevens and Fox 1991; Holtmeier 2009; Körner 2012). Climate warming is expected to induce treelines to advance to higher elevations. Empirical studies in diverse mountain ranges, however, give evidence of both advancing alpine treelines as well as rather insignificant responses (Baker and Moseley 2007; Hofgaard et al. 2009; Wieser et al. 2009; Grigor'ev et al. 2013; Shrestha et al. 2014; Chhetri and Cairns 2015), pointing to an evident research deficit. Harsch et al. (2009) analysed data from 166 globally distributed treelines which dynamics were monitored since AD 1900. 47 % of the treelines did not show any elevational shift while 52 % of the treelines advanced to higher altitudes and only 1 % showed recession. Apart from climate change, land use changes influence high altitude vegetation patterns and treeline positions (e.g. Dirnböck et al. 2003; Bolli et al. 2007; Gehrig-Fasel et al. 2007; Pauchard et al. 2009; Schickhoff 2011; Penniston and Lundberg 2014; Piermattei et al. 2014; Durak et al. 2015). Thus there is the need to disentangle these effects to draw correct conclusions concerning the sensitivity of treelines to climate change.

Many studies detected above-average current warming trends between 0.6 and 1°C per decade for the Himalayan region. Maximum values were found for the high elevations and during winter and pre-monsoon seasons (Shrestha et al. 1999; Liu and Chen 2000). For the Rolwaling valley, the target area of the present study, monthly temperature trends in the order of 0.7 °C per decade were assessed in winter and pre-monsoon seasons (Gerlitz et al. 2014). During monsoon, no statistically significant trends were identified. Trend analyses of precipitation amounts in the Himalayas do not show a consistent pattern. Some studies, however, detected negative trends of winter and pre-monsoon precipitation over the western and central Himalaya (Duan et al. 2006; Bhutiyani et al. 2010; Jain et al. 2013). An enhanced frequency of winter and pre-monsoon drought events was reported for western Nepal by Wang et al. (2013). Recent climatic changes will inevitably affect growth patterns and seedling performance at Himalayan treelines, albeit to a regionally differentiated extent (Schickhoff et al. 2015, 2016).

It is widely accepted that climate exerts a top-down control on local ecological processes at the treeline (e.g. Batllori and Gutiérrez 2008; Elliott 2011). However, it is not well understood how landscape scale and local scale abiotic and biotic factors and processes interact and influence the treeline and its response to climate change. Moreover, effects of climate warming often mix up with impacts of land use (Malanson et al. 2007; Batllori et al. 2009). In consequence, complex research approaches at local and landscape scales at natural treelines are needed (e.g. Malanson et al. 2011). Recent studies based on a global treeline data set suggest a close link between treeline form (spatial pattern) and dynamics. Harsch and Bader (2011) consider treeline form (diffuse, abrupt, island, krummholz) to be an indicator of controlling mechanisms (at the levels of direct tree performance, causative stresses, and modifying neighbour interactions) and response to climate change. They confirmed the link between treeline form and dynamics established earlier (Lloyd 2005; Harsch et al. 2009), and supported the general suitability of treeline form for explaining the variability of response to climate warming. Apart from treeline form, tree species composition, tree density, diameter and height distributions can be indicators for treeline sensitivity to climate change. In addition, these parameters provide information on the establishment of recruits and their performance which are among the most significant indicators of treeline sensitivity (Germino et al. 2002; Holtmeier 2009; Körner 2012; Zurbriggen et al. 2013; Schickhoff et al. 2015, 2016).

In the Himalaya, only very few studies on treeline seedlings have been conducted so far, and tree recruitment in treeline ecotones is not well understood (Schickhoff 2005; Shi and Wu 2013; Dutta et al. 2014; Schickhoff et al. 2015, 2016). Hitherto available studies refer to treeline ecotones with deviating species compositions and population structures, and generally to ecotones which have been disturbed by land use effects (e.g. Shrestha et al. 2007; Ghimire et al. 2010; Gaire et al. 2011; Sujakhu et al. 2013; Shrestha et al. 2014; Chhetri and Cairns 2015). Thus, their generalizability and informative value for near-natural treeline ecotones is limited. The present study was conducted in the framework of the research scheme TREELINE which focuses on spatially differentiated patterns and processes by correlating varied treeline responses to landscape- and local-scale site conditions and mechanisms (geomorphic controls, soil physical and chemical conditions, plant interactions associated with facilitation, competition, and feedback systems). We present population structures from a near-natural treeline ecotone in Rolwaling Himal, Nepal, focussing on species compositions and growth parameters with an emphasis on the ratio of recruits to adult trees. Unlike most other treeline studies in Nepal (e.g., Shrestha et al. 2007; Lv and Zhang 2012; Sujakhu et al. 2013; Gaire et al. 2014) we assessed the treeline forming tree species of our study area in its entirety as, e.g. Miehe (1990) and Miehe and Miehe (2000) did. Near-natural treeline ecotones can contain co-dominant tree species which respond differentiated to climate change (Trant and Hermanutz 2014). In consequence, multispecies approaches to treeline dynamics, which survey all ecotone tree species, can capture the sensitivity of the ecotone to climate change sufficiently. We aim at i) analyzing species-specific patterns and abruptness of transitions of tree and recruit densities and growth parameters along the elevational gradient, ii) detecting altitudinal boundaries of tree species distributions, and iii) assessing the relation between abrupt changes of growth parameters and temperature gradients along the altitudinal zoning of the ecotone and relating the results to the sensitivity to climate warming. We hypothesize that changes in tree physiognomy (diameter at breast height (dbh), tree height, growth forms) and density occur species-specific and with varying abruptness intensities along the treeline ecotone, indicating complex spatial structures, and resulting in several tree species limits inside the ecotone, each potentially susceptible to climate change. Air and soil temperatures are supposed to be crucial variables explaining species-specific responses.

16.2 Materials and Methods

16.2.1 The Study Area

The Rolwaling valley (27°52’ N; 86°25’ E) is located in Dolakha District, east-central Nepal, adjacent to the border to Tibet Autonomous Region. It is embedded in the Gaurishankar Conservation Area (2035 km^2), which has been a protected area since 2010 (Shrestha et al. 2010; Bhusal 2012). Our study site is located at a north facing slope ranging from the closed subalpine forest via timber- and treeline to the lower alpine vegetation zone (3740 m to 4250 m a.s.l.). We subdivided the study site into three slope sectors according to their deviating exposure (Fig. 16.1).

Due to the remote location without connection to the road network (three days walking distance), the small human population, and the fact that plants and animals in Rolwaling are protected to a certain extend by the recurring Buddhist theme of a sacred hidden valley (Sacherer 1979; Baumgartner 2015), the Rolwaling treeline exhibits a near-natural state (cf. section 16.3.6) and represents a climatic treeline. The study slopes show no signs of fire or of grazing by cattle, wood cutting is negligible. The Rolwaling River separates the uninhabited north-facing study slope from the very sparsely populated south-facing slope where human impact is likewise low. Thus, in view of the fact that most Himalayan treeline sites are disturbed by land use effects (Schickhoff et al. 2015, 2016), the study slopes provide a unique research opportunity for detecting a climate change signal when assessing treeline dynamics.

The study sites cover the entire treeline ecotone. The lower reaches contain mixed forest stands with the upper limits of tall, upright growing individuals of *Acer caudatum, Abies spectabilis* and *Betula utilis*. A krummholz belt with dense and largely impenetrable *Rhododendron campanulatum* thickets represents the transition to alpine dwarf scrub heaths with only small (dbh < 7 cm) and stunted tree species individuals (Fig. 16.2).

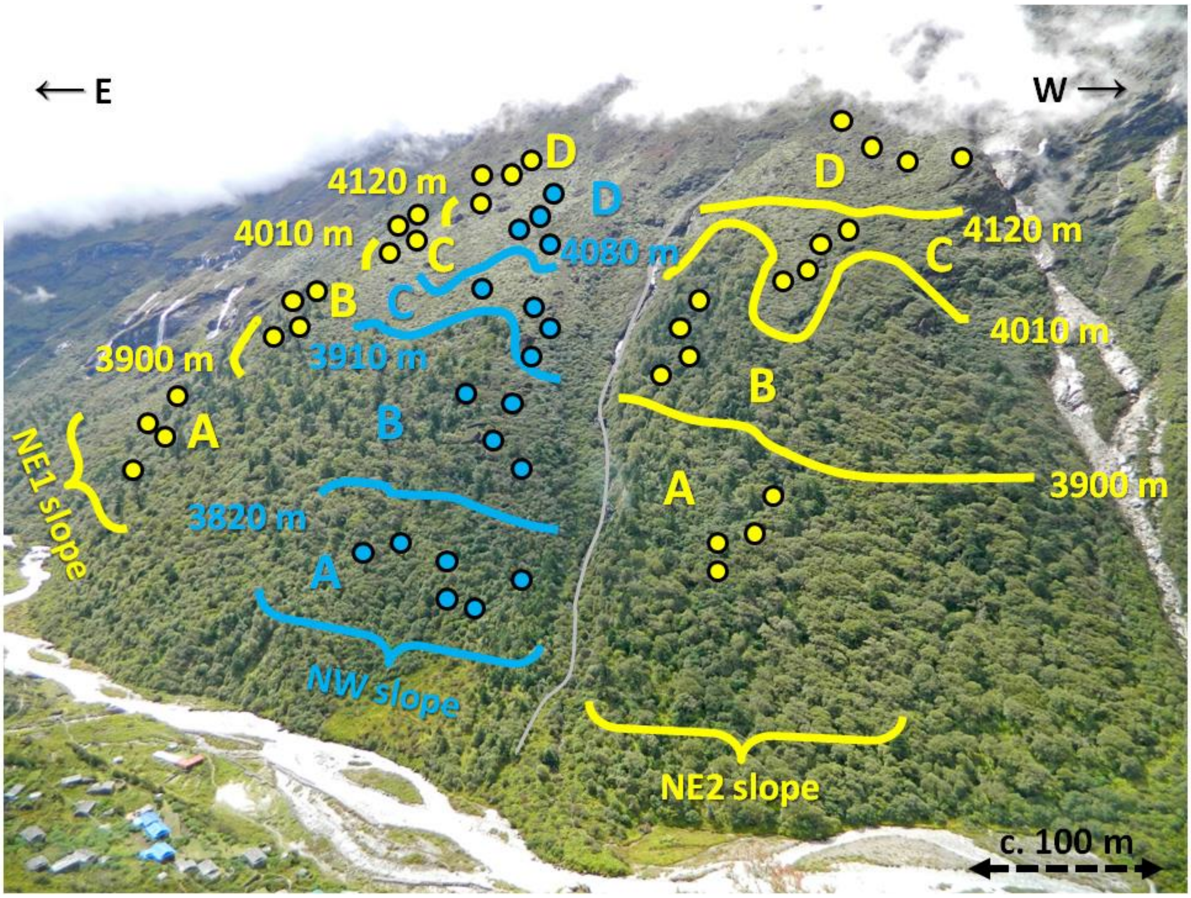

Fig. 16.1 Stratification of the study area by altitude (zones *A*, *B*, *C*, *D*) and aspect (NE, NW) and approximate location of plots (*blue* and *yellow points*) (Source: Niels Schwab, 18 September 2014)

16.2.2 Data Collection

We stratified the treeline ecotone according to the altitudinal zoning of tree species composition and stand structure into 4 altitudinal zones, reaching from closed forests (zone A) to alpine dwarf scrub heaths (zone D; Table 16.1). We established a total of 50 plots, each with a size of 20 x 20 m² (projected on a horizontal plain), comprising 4 randomly selected plots in each of the zones A – D at three slopes (two slopes NE-exposed, one slope NW-exposed; Table 16.1). We identified the tree species (nomenclature according to Press et al. 2000), in doing so we conceived *S. microphylla* as an aggregate, comprising potentially occurring and hybridizing *S. microphylla* and *S. foliolosa*. We measured dbh with a diameter measuring tape at 1.3 m above ground level (Van Laar and Akça 2007), and height of all trees with dbh ≥ 7 cm with a laser dendrometer (Laser Technology Criterion RD 1000, distance measurement: MDL LaserAce 300). Individuals of tree species with dbh < 7cm (recruits) were identified, counted and assigned to height classes (Table 16.2). We counted all stumps ≥ 7 cm diameter and measured diameters 10 cm above ground, or, if stump height was less than 10 cm, at highest point above ground. We identified the species and cause of death (natural, anthropogenic, unidentified) in each plot. We classified the degree of decomposition of tree stumps into 4 classes (undecomposed; slight, medium, intense decomposition) to roughly estimate the dieback period (Schickhoff 2002). We assumed the intensely decomposed stumps to not influence the current stand structure. Vegetation surveys took place in April, Mai, July and August 2013, and September 2014.

To relate soil temperature to growth parameters we installed 34 modified WiFi Plant sensors (Koubachi AG), which have monitored soil temperature in 10 cm depth in a one-hour interval since May 2013. For this paper we use data from June 2013 to May 2014. 32 sensors were placed on the NW-exposed and on one of the NE-exposed slopes (2 transects x 4 altitudinal zones x 4 plots). Mobile climate stations installed in the lower and upper part of the ecotone have recorded air temperatures since April 2013 (data evaluated until June 2014). Soil bulk density of field-moist soils was sampled using soil core cutters (100 cm^3), and analysed following DIN EN ISO 11272:2014. Additional, atmospheric nitrogen deposition (NO_2, NH_3) was measured using passive devices (Passam AG) requiring no power for their operation. The samplers were placed in a special shelter 2 m above ground to protect them from rain and minimise wind influence. Exposition time was two weeks.

Fig. 16.2 Transition from closed forest to alpine dwarf scrub heath. (**a**) Uppermost stand of *A. spectabilis* at NE-slope (c. 4000 m a.sl.); (**b**) *Rh. campanulatum* krummholz (in *white-pink* bloom) and transition to *Abies-Betula* forest (zone B); (**c**) Elevational range from zone A to D with transition from B to C in focus; (**d**) Mixed forest stand of zone B and abrupt transition to *Rh. campanulatum* krummholz belt; (**e**) *Rh. campanulatum* krummholz (front) and abrupt transition to mixed *Abies-Betula* forest of zone B; (**f**) Alpine dwarf scrub heath with *Rh. campanulatum* and *Rhododendron* dwarf shrub species and single *S. microphylla* individuals (**a–c**: 5 May 2013; **d**: 23 July 2013; **e–f**: 17 September 2014) (Source: Niels Schwab)

Table 16.1 Study site properties

	Aspect	Zones			
		A	B	C	D
Slope 1	NE				
Altitude [m a.s.l.]		3830-3895	3920-3990	4015-4080	4180-4245
No. of plots		4	4	4	4
Slope 2	NE				
Altitude [m a.s.l.]		3795-3875	3925-3990	4040-4090	4130-4225
No. of plots		4	4	4	4
Slope 3	NW				
Altitude [m a.s.l.]		3770-3795	3845-3890	3925-4020	4140-4200
No. of plots		6	4	4	4
Total no. of plots		14	12	12	12
NE transition altitudes [m a.s.l.]		3900 (AB)	4010 (BC, TL)	4120 (CD)	
NW transition altitudes [m a.s.l.]		3820 (AB)	3910 (BC, TL)	4080 (CD)	
Vegetation		Mixed forest	Mixed forest	Krummholz	Alpine scrubs

Aspects: *NE* north-east, *NW* north-west, *TL* treeline

Table 16.2 Size classifications of tree species individuals and abruptness parameters

dbh [cm]	Height [m]	Recruit class	Terms		Indication of abruptness for
<7	0-10	1	Seedlings	Recruits	Height, density
<7	11-50	2			
<7	51-130	3	Saplings		
<7	131-200	4			
<7	201-	5			
<7	ns	-		Trees	dbh, height, density

dbh diameter at breast height, *ns* not specified

16.2.3 Data Analyses

We computed stem numbers and stand densities per hectare (ha), and visualized population structures and species compositions by plotting barplots and histograms of all samples and subsamples. Comparisons of our density diameter distributions to other studies should be understood as only rough estimates due to the differing study specific definitions of size classes and classification intervals. In order to analyse regeneration patterns we calculated values for the mean height of recruits as mean of the class configurations. We calculated a regeneration index (*RI*) according to Schickhoff (2002):

$$RI = \sum_{i=1}^{5} \bar{x}_{med(i)} n_i$$

where n_i is the number of recruits in the 5 recruit height classes (Table 16.2) and $\bar{x}_{med(i)}$ is the median of the height class limits. In contrast to mean height values of recruits, the *RI* includes information of abundance and combines it with the recruits' height. Thus the *RI* provides information on growth performance and success of establishment beyond the seedling stage.

In order to describe and analyse variation in stand structures and to characterize abrupt or smooth/gradual transition patterns along the ecotone, we calculated the abruptness of transitions between subsequent zones ($\text{abruptness}_{\text{AB}}$, $\text{abruptness}_{\text{BC}}$, $\text{abruptness}_{\text{CD}}$). We computed the abruptness for various parameters (Table 16.2) using a modified approach by Wiegand et al. (2006) and Batllori and Gutiérrez (2008). The abruptness of the transitions was the difference of the scaled values of successive zones (lower zone minus upper zone; scaled range [0,1]):

$$abruptness_{lh} = \frac{\bar{x}_{arith(l)} - min_l}{max_l - min_l} - \frac{\bar{x}_{arith(h)} - min_h}{max_h - min_h}$$

where *l* and *h* are the altitudinal zones (*A*, *B*, *C*, *D*). The lower zone (e.g. *A*) is denoted *l* and the successive higher zone (e.g. *B*) is denoted *h*. A positive abruptness indicates a transition of decreasing values with elevation as it is generally expected in a treeline ecotone while a negative abruptness points to an increasing value of a stand parameter with elevation (see Table 16.3 for further differentiation of abruptness values). Total abruptness was gained as the arithmetic mean abruptness of all parameters under consideration at a specific transition. We calculated both the abruptnesses for all individuals of the stands, and the species-wise abruptnesses.

Table 16.3 Definitions and interpretation of abruptness values

Abruptness	Definition/interpretation
-1,…,1	Maximum range
Positive	Decreasing parameter with elevation
Negative	Increasing parameter with elevation
-1	Transition from maximum to zero
-1	Transition from zero to maximum
0	No change
1/3 resp. -1/3	Linear transition in case of 4 zones
-0.33 ≤ abruptness ≤ 0.33	Gradual/smooth transition
-0.5 ≥ abruptness ≥ 0.5	Abrupt transition, change by half or more of the parameters range
0.33,…,0.5 resp. -0.33,…,-0.5	Intermediate transition

Seasonal means for discrete time steps (0, 6, 12, 18 h local time) were calculated for air temperature for each climate station. Topographically induced 6-hourly temperature lapse rates ($\Delta T/\Delta Z*100$) were derived for the NW and NE transects to assign site specific air temperatures (Gerlitz et al., this volume). We calculated growing season mean soil temperature at treeline and number of growing degree days according to Körner and Paulsen (2004). For soil temperatures we calculated abruptness values according to the above described procedure for mean annual and mean seasons' temperatures (MAM, JJAS, ON, DJF). All computations and figure plottings were carried out using 'base' and 'graphics' R functions (version 3.1.2; R Core Team 2014) and the packages 'plyr' (Wickham 2011) and 'vegan' (Oksanen et al. 2014).

16.3 Results

16.3.1 General Vegetation Patterns and Species Limits

In general, upper subalpine forests are primarily composed of *B. utilis* and *A. spectabilis*, with *Rh. campanulatum* and *Sorbus microphylla* forming a second tree layer. Closed forests give way to an extensive krummholz belt of *Rh. campanulatum* at c. 3910 m a.s.l. (NW) / 4010 m a.s.l. (NE), which turns into alpine *Rhododendron* sp. dwarf scrub heaths at c. 4080 / 4120 m a.s.l. (Fig. 16.2). Total plant species richness decreases from the closed forests in the subalpine zone across the treeline ecotone and increases again in the uppermost dwarf scrub heath plots of zone D at the transition to alpine grassland. Minimum species numbers are found in the krummholz belt zone C with a mean species number of 12 and in the lower dwarf scrub heath plots with 11 species. Zone A contains the maximum of 25 plant species (unpublished data by B. Bürzle).

We identified different tree species-specific altitudinal limits (i.e. “the uppermost occurrence regardless of size”, Körner 2012) throughout an altitudinal gradient from zone A to zone D (Fig. 16.3): We found the uppermost individuals of *Prunus rufa* at 3925 m a.s.l. (NE) resp. 3890 m a.s.l. (NW) in zone B, of *A. caudatum* at 3950 m a.s.l. (NE) resp. 3890 m a.s.l. (NW) in zone B, and of *J. recurva* at 4080 m a.s.l. (NE, no *J. recurva* at NW) in zone C. All other species still occurred in zone D. We found *B. utilis* recruits at 4140 m a.s.l. in the lowest plot in zone D at the NW slope, but in none of the higher plots. Thus the species limit of *B. utilis* appears to be at the lower part of zone D. In contrast, we found *A. spectabilis* individuals even at 4185 m a.s.l. Similarily, *S. microphylla* and *Rh. campanulatum* occur at nearly all plots in zone D (both maximum altitude 4245 m a.s.l.). In consequence, it is not possible to set their exact altitudinal limits and the position of the tree species line (i.e. “the elevational limit of the uppermost occurring tree species”, Körner 2012). Few plant sociological samplings above zone D point to a position of the tree species line at the upper border of zone D (c. 4260 m, unpublished data by B. Bürzle, Fig. 16.3).

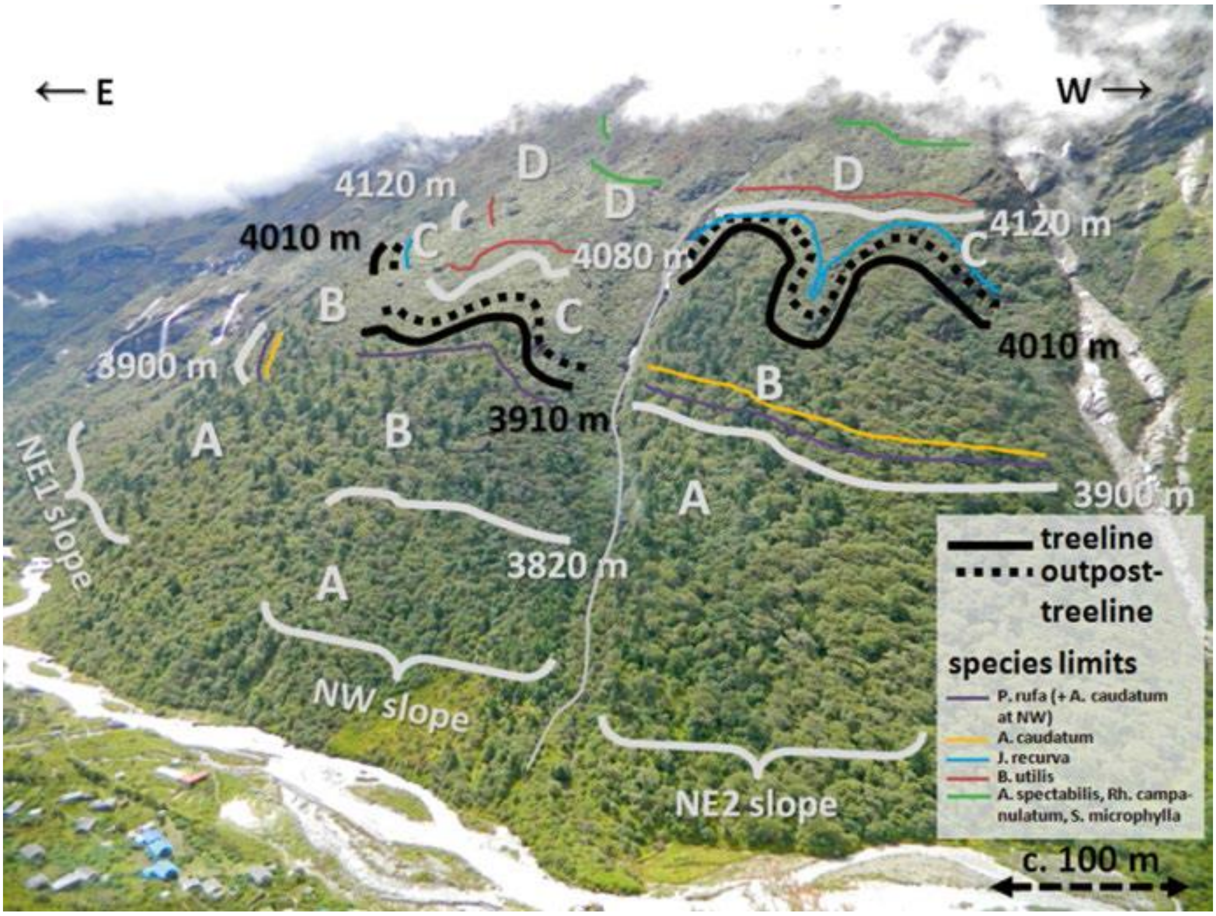

Fig. 16.3 Approximate locations of treeline, outpost-treeline and species limits (Source: Niels Schwab, 18 September 2014)

16.3.2 Tree Species Composition

The lowest zones A and B contain mixed forest stands where tall, upright growing, adult individuals of most tree species reach their upper limits (*A. caudatum* in A; *A. spectabilis*, *B. utilis* and *P. rufa* in B). Zone C represent the krummholz belt with dense and largely impenetrable *Rh. campanulatum* thickets and upper limits of stunted *A. spectabilis* and *B. utilis* tree individuals with dbh ≥ 7 cm. Zone D is occupied by alpine vegetation (mainly dwarf scrub heaths), interspersed with only low growing individuals or young growth (dbh < 7 cm) of *A. spectabilis*, *B. utilis*, and *Rh. campanulatum* (Fig. 16.2). We found very few *S. microphylla* individuals with dbh ≥ 7 cm in zone D (Figs. 16.4 and 16.5). The recruit density pattern (Fig. 16.6) mostly resembled the one of individuals with dbh ≥ 7 cm. The occurrence of *Juniperus recurva*, a species that can grow to tree size, remarkably differed between recruits and adults. We found no individual with dbh ≥ 7 cm, *J. recurva* recruits were existent in zones A, B and C. *Rh. campanulatum* and *S. microphylla* seedlings occurred in rather high abundance in zone D, however no tree-sized individual of these species was detected. We found the highest number of individuals of both trees and recruits in zone B. Zone C exhibited nearly the same number of trees per ha as zone B. Zones A and C resembled each other in terms of recruit numbers, whereas recruit density indicated distinct differences between both zones and zone B. However, altitudinal zones differed in the percentages of the individual species. *P. rufa* and *J. recurva* individuals occurred in very low abundance and are thus not analysed in detail.

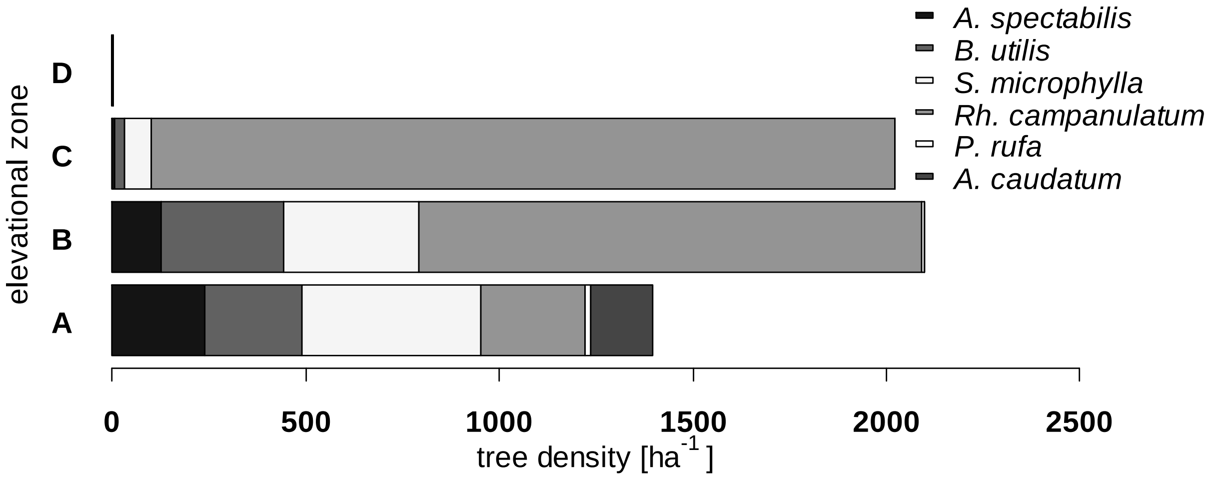

Fig. 16.4 Tree species density of individuals ≥ 7 cm dbh (trees) (Source: Niels Schwab)

All tree species occurring in zone A except the rare *P. rufa* exhibited evenly distributed numbers of individuals. *Rh. campanulatum* becomes more frequent with elevation. In zone C, *Rh. campanulatum* dominates the tree species composition and is accompanied by few *Sorbus* individuals. Although *Rh. campanulatum* accounts for more than 50 % of tree individuals and more than 75 % of recruits in zone B, the transition from zone B to C shows the most abrupt change in tree species composition along the altitudinal gradient. This abrupt change in species composition coincides with the most abrupt changes in annual and seasonal mean soil temperature at transition BC (cf. section 16.3.7). *S. microphylla* occurred with high constancy and its density diameter distribution points to an established population in zone C, which coexists aside the *Rh. campanulatum* population. Established recruit populations in zone D indicate the potential of *Rh. campanulatum* and *S. microphylla* to sprout and survive at least the early life stages at this high altitude (see discussion 16.4.3).

16.3.3 Stand Densities

Stand densities showed similar patterns in zones A, B and C: We found 7473 (zone A, standard deviation SD=4432), 8748 (zone B, SD=6718) and 7280 (zone C, SD=3948) individuals per ha belonging to the recruit class (dbh < 7cm) (Figs. 16.6 and 16.7). The number was significantly smaller in zone D. Here, 1333 individuals per ha (SD=1197) represent more than one tree species recruit individual per 10 m² in the alpine dwarf scrub heath. However, zone D exhibited only two tree individuals per ha in the 7 –14 cm dbh class, and not a single individual of higher dbh classes. The number of trees in the dbh class 7 – 14 cm increased continuously with elevation from 984 trees per ha (SD = 386) in zone A to 1597 (SD= 869) in zone B, and to 1943 (SD = 1246) in zone C. The following class (14-21 cm dbh) showed most individuals in zone A and B (258 resp. 283 trees per ha, SD = 157 resp. SD = 177), and only 73 trees per ha (SD=104) in zone C. In the latter we sampled four trees per ha (SD = 9) in the 21-28 cm class; trees did not exceed 28 cm dbh. The number of individuals per class decreased with increasing dbh in zones A and B. All dbh classes in zone B revealed higher numbers of trees and recruits compared to zone A. Old trees exceeding 49 cm dbh doubled in number in zone B (31) compared to zone A (14, not shown in Fig. 16.7). The largest dbh were 114 cm in zone A and 113 cm in zone B.

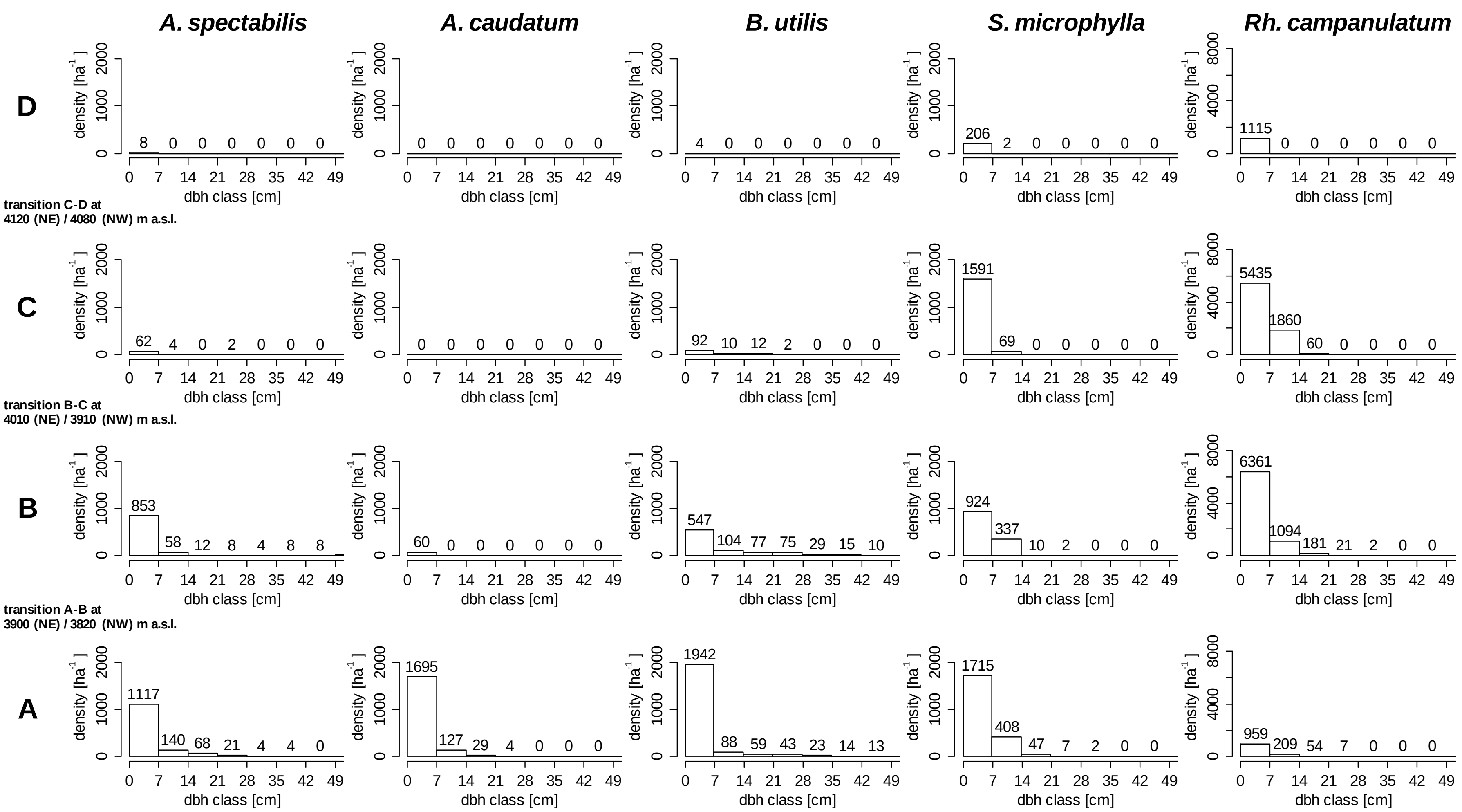

Fig. 16.5 Species-wise density-diameter distribution of the most abundant tree species in the altitudinal zones A, B, C and D. Only classes < 49 cm dbh are printed. Note differences in scaling of *Rh. campanulatum* y-axis (Source: Niels Schwab)

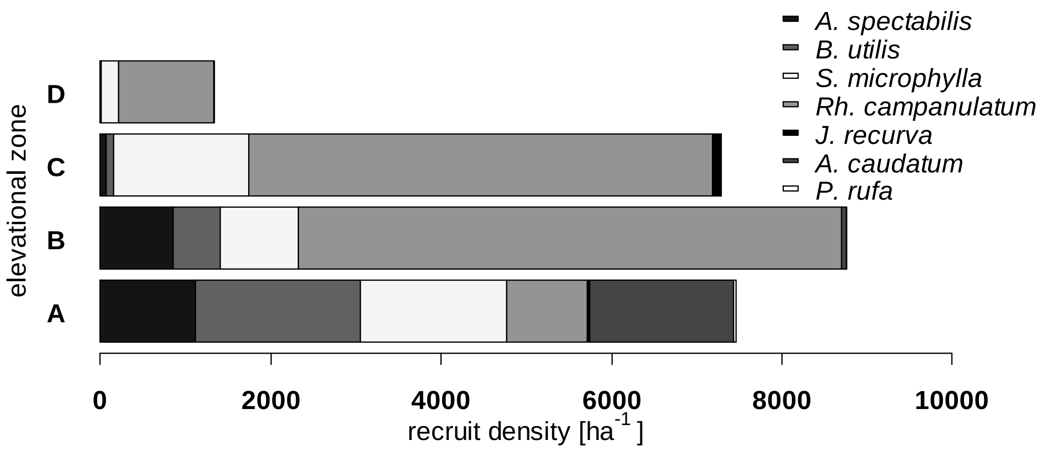

Fig. 16.6 Tree species density of individuals < 7 cm dbh (recruits) (Source: Niels Schwab)

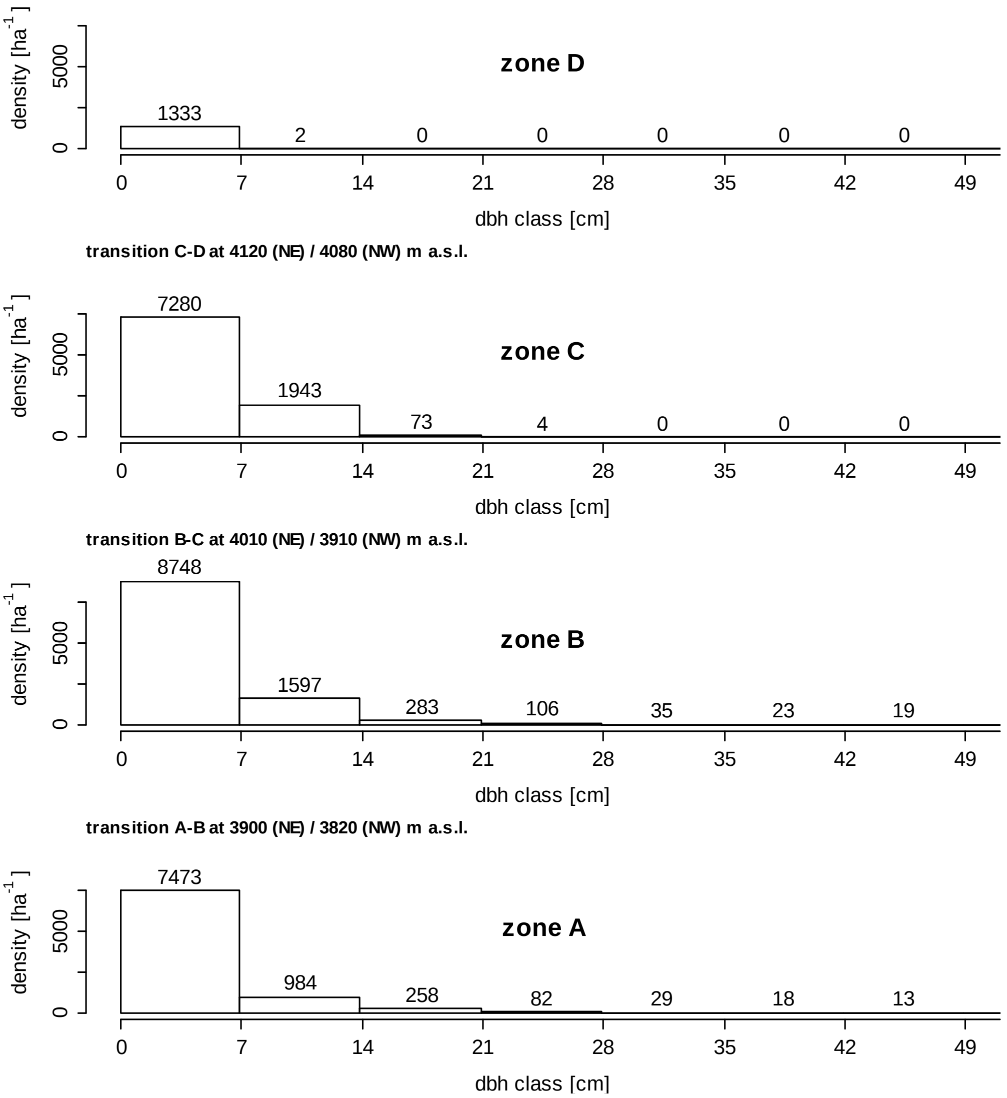

Fig. 16.7 Density-diameter distribution of all tree species in the altitudinal zones A, B, C and D. Only classes < 49 cm dbh are printed (Source: Niels Schwab).

16.3.4 Tree Species Population Structures and Regeneration

16.3.4.1 Density-Diameter Distributions

The different tree species *A. spectabilis, A. caudatum, B. utilis, S. microphylla*, and *Rh. campanulatum* showed species-specific deviations from a basically similar density-diameter distribution (Fig. 16.5). A common characteristic is the reverse J-shape of the density-diameter distributions with significantly higher numbers of recruits in comparison to numbers of all other dbh classes. We found recruits only but no trees in nearly all uppermost reaches of each species' occurrences.

A. spectabilis: *A. spectabilis* exhibited high numbers of recruits < 7 cm dbh in relation to the larger dbh classes in zones A and B. In general, this holds also for zone C, however recruit (62 per ha, SD = 120) and tree (6 per ha, SD=12) abundances were very low and we did not find trees exceeding 22.8 cm dbh. In zone D only eight *A. spectabilis* recruits per ha (SD = 22) occurred, and no individuals with dbh > 7 cm. The number of trees exceeding 49 cm dbh differed in zones A and B: We found only four trees per ha in A and 27 per ha in B.

A. caudatum: *A. caudatum* occurred in zones A and B only, and showed a high abundance of recruits (1695 per ha, SD = 1641) and tree individuals up to the dbh class 21-28 cm. No *A. caudatum* trees > 7 cm dbh were detected in zone B, but 60 recruit individuals per ha (SD = 85).

B. utilis: Similar to *A. spectabilis*, the population structure of *B. utilis* differed with altitude: We found a high number of recruits in zone A (1942 per ha, SD = 1627) and decreasing abundances in larger dbh classes. In contrast to *A. spectabilis, B. utilis* exhibits a higher number of trees in all classes from 7 to 42 cm dbh in zone B. Further, the number of *B. utilis* exceeding 42 cm dbh is higher in zone A (24 per ha) compared to B (14 per ha). The absolute number of *B. utilis* recruits in zone B (547 per ha, SD = 611) is smaller compared to *A. spectabilis* recruits, and the ratio of recruits to trees is smaller due to the higher number of individuals in the tree classes > 7 cm dbh. In zone C, *B. utilis* showed 92 recruits per ha (SD = 219) and tree individuals in higher number and larger dbh's than *A. spectabilis*. We found merely four *B. utilis* recruits per ha (SD = 14) in zone D.

S. microphylla: *S. microphylla* recruits are of high abundance in zones A (1715 per ha, SD = 1248), B (924 per ha, SD = 798) and C (1591 per ha, SD = 2064). In zone A, *S. microphylla* tree individuals occurred only up to the dbh class 28-35 cm. *S. microphylla* is the only species with a substantial number of individuals in zone C, apart from *Rh. campanulatum* (see below). Even 206 recruits per ha (SD = 297) were present in zone D.

Rh. campanulatum: The population structure of *Rh. campanulatum* differed significantly from other species: In zone A, the number of recruits (959 per ha, SD = 1180) and trees per ha were in the same range as other species. *Rh. campanulatum* recruits exhibited significantly higher abundances of recruits in zones B (6361 per ha, SD = 5893), C (5435 per ha, SD = 2395) and D (1115 per ha, SD = 963). This prolific regeneration was followed by correspondingly high abundances in the subsequent dbh classes. However, *Rh. campanulatum* populations were poor concerning maximum dbh, which was 22.5 cm in zone A, 29.8 cm in zone B, and 18.7 cm in zone C. In zone D, we found only recruits < 7 cm dbh. Zone C exhibited a much more homogeneous all-species configuration of the 7 to 14 cm dbh class due to the high percentage *Rh. campanulatum* individuals, and less recruits per ha compared to zone B. Altitudinal transitions in *Rh. campanulatum* populations did not follow the trend of other species in terms of decreasing dbh and abundance with elevation (cf. Fig. 16.5). The smaller SD values of *Rh. campanulatum* recruit densities in zones B, C and D indicate that *Rh. campanulatum* population is spatially more homogenous intra-zone than recruit populations of other species. In contrast to zone A, *Rh. campanulatum* accounts for the significantly higher all-species tree densities in zones B and C (Fig. 16.4).

Total all-species recruit densities of zones A, B and C did not differ as much as the tree densities. All species show L- or reverse J-shaped density-diameter distributions (Fig. 16.5). At some altitudinal zones, several species exhibit a very pronounced L-shape indicating an over-proportional number of recruits compared to the classes above 7 cm dbh, e.g. *A. caudatum* and *B. utilis* in zone A and *S. microphylla* in C. Zone A contains more recruits of *A. spectabilis*, *B. utilis* and *S. microphylla* compared to zone B, where their recruit numbers are distinctly lower compared to tree densities (Figs. 16.4, 16.5 and 16.6).

In summary, we assessed largely prolific regeneration of all tree species. Seedling establishment of *B. utilis*, *A. spectabilis*, and *S. microphylla* occurred to some extent far above the upper limit of adult trees. Some individuals of more than 2m height even grew vigorously above the krummholz belt, where a small birch tree of 1.7 m in height was found in 4140 m a.s.l. Maximum recruit density occurred between 3920 and 3990 m a.s.l. (NE) resp. 3845 – 3890 m a.s.l. (NW) in zone B (more than 8700 N ha^{-1}), where *Rh. campanulatum* showed most intense recruitment (more than 6300 N ha^{-1}). Seedling/sapling density sharply decreased towards the alpine tundra (zone D), where only *Rh. campanulatum* and to some extent *S. microphylla* recruits occurred with considerable numbers of individuals.

16.3.4.2 Recruit Heights

The height class distributions of recruits showed clear variations between species and between altitudinal zones (Fig. 16.8). *A. spectabilis* exhibited reverse J-shaped distributions in zones A and B, whereas the small numbers of recruits in zones C and D were rather homogenously distributed among classes. For *A. caudatum*, we found a high percentage of tall recruits exceeding 2 m height and a slight increase in individual numbers from the 10 cm to 200 cm height classes in zone A. An evenly distributed small number of *A. caudatum* recruits occurred in zone B which was absent in zones C and D. *B. utilis* recruits showed a heterogeneous distribution between height classes with a relative small number of seedlings smaller than 10 cm in height in zone A. In zone B, the taller height classes exceeding 50 cm had higher recruit densities. The same holds for zone C, however with distinctly smaller recruit numbers. In zone D, we found four *B. utilis* recruits per ha exclusively in the height class of 131 to 200 cm. *S. microphylla* showed increasing class sizes with increasing recruit heights in zones A, B and C, except for the 10 cm class in zone B which contained c. three times more recruits than the subsequent 50 cm class. The distribution of *S. microphylla* recruits in zone D corresponds to a bell shape with no individuals smaller than 10 cm. *Rh. campanulatum* exhibited a reverse J-shape in zone A, and a reverse L-shape with the overall highest number of recruits in any class in zone B with c. 4400 per ha in the ≤ 10 cm class. The height class distribution in zone C was rather homogenous, while it resembled the bell shape in zone D.

The average recruit height of all tree species was tallest in zone C followed closely by mean height in zone A (Fig. 16.9, black dotted line). Likewise, the recruits of most single species reached their maximum height in zone C. In general, recruits of *P. rufa*, *B. utilis*, *S. microphylla* and *A. caudatum* showed a mean height of more than 130 cm, which is taller than the recruit mean height of *J. recurva*, *Rh. campanulatum* and *A. spectabilis* in all altitudinal zones. Recruits of all species in zone D showed a lower height growth compared to zone C, except for *B. utilis*, whose recruit height increased slightly. *B. utilis* was the only species with a continuous, however gentle increase in mean recruit height with elevation. The average height of *B. utilis* and *S. microphylla* recruits were distinctly taller than *A. spectabilis* and *Rh. campanulatum* recruits in zone D (cf. Fig. 16.9). *S. microphylla* recruits' height did not change distinctly along the altitudinal gradient. The height of *Rh. campanulatum* recruits exhibited highest values in zone C and smallest in zone B (in average < 50 cm). *A. spectabilis* recruits showed compared to other species smallest heights in all zones except in zone B where *Rh. campanulatum* recruits did not reach the height level of *A. spectabilis*. Nevertheless, the mean height of *A. spectabilis* recruits increased constantly with elevation up to zone C (cf. Fig. 16.9).

16.3.4.3 Regeneration index (*RI*)

The regeneration index (*RI*) of the recruits of all species showed the highest value in zone A, followed by C, B, and D (Fig. 16.10, black dotted line). The single species showed different *RI* patterns: *Rh. campanulatum* exhibited the most conspicuous values along the altitudinal gradient with a rather low *RI* in zone A, and a *RI* higher than any of the other species in zones B, C, and D (Fig. 16.10). Like *Rh. campanulatum S. microphylla* shows a non-uniform *RI* trend along the gradient with the second highest *RI* level of all species in zones B, C and D (Fig. 16.10). The *RI* reached nearly 130,000 in zone C while the maximum of all other species except *Rhododendron* was only 7000 (*B. utilis*). In contrast to *S. microphylla*, the *RI* value of *A. caudatum* was very low in zone B. The *RI*s of *B. utilis* and *A. spectabilis* constantly decreased towards zone D (Fig. 16.10). For instance, *A. spectabilis* showed a value of 25,000 in zone A, 20,000 in B and only 2400 and 260 in zones C and D. *J. recurva* and *P. rufa* showed the overall smallest *RI* values in zones A and B (Fig. 16.10).

Depending on the regeneration indicator in focus, different species seem to perform better at different altitudinal positions. While the mean height (Fig. 16.9) shows if the population of a species is able to reach a specific mean sprout height the *RI* (Fig. 16.10) provides information on the actual performance of the recruits of a species by incorporating their abundance. Comparing values of both indicators, it becomes obvious that the height–abundance patterns of the different species are complex and non-uniform. The small *RI* values of *B. utilis* in zones C and D contrast with their high mean heights. Obviously *B. utilis* recruits are able to grow at these altitudes but they do not grow in considerable abundance. On the other hand, *A. spectabilis* recruits with similar very low *RI* values in C and D grow up to a considerably lower height only, the lowest of all species in zones C and D. These relations indicate a comparatively better performance of *B. utilis* at these high elevation environments. Both height and RI of *S. microphylla* exhibited high and even highest values and we even found rare tree individuals ≥ 7 cm dbh in zone D. The dbh classes above 14 cm dbh include only small numbers of *S. microphylla* in the lower zones (Fig. 16.5). *Rh. campanulatum* exhibited an enormously high *RI* and highest *Rhododendron*-specific mean height together with the absolute dominance in zone C (Figs. 16.4 and 16.6). In zone D, *Rh. campanulatum*’s heights are lower, and we did not find any individuals ≥ 7 cm dbh among the number of 1115 recruits per ha, which is more than five times the abundance of *S. microphylla* recruits.

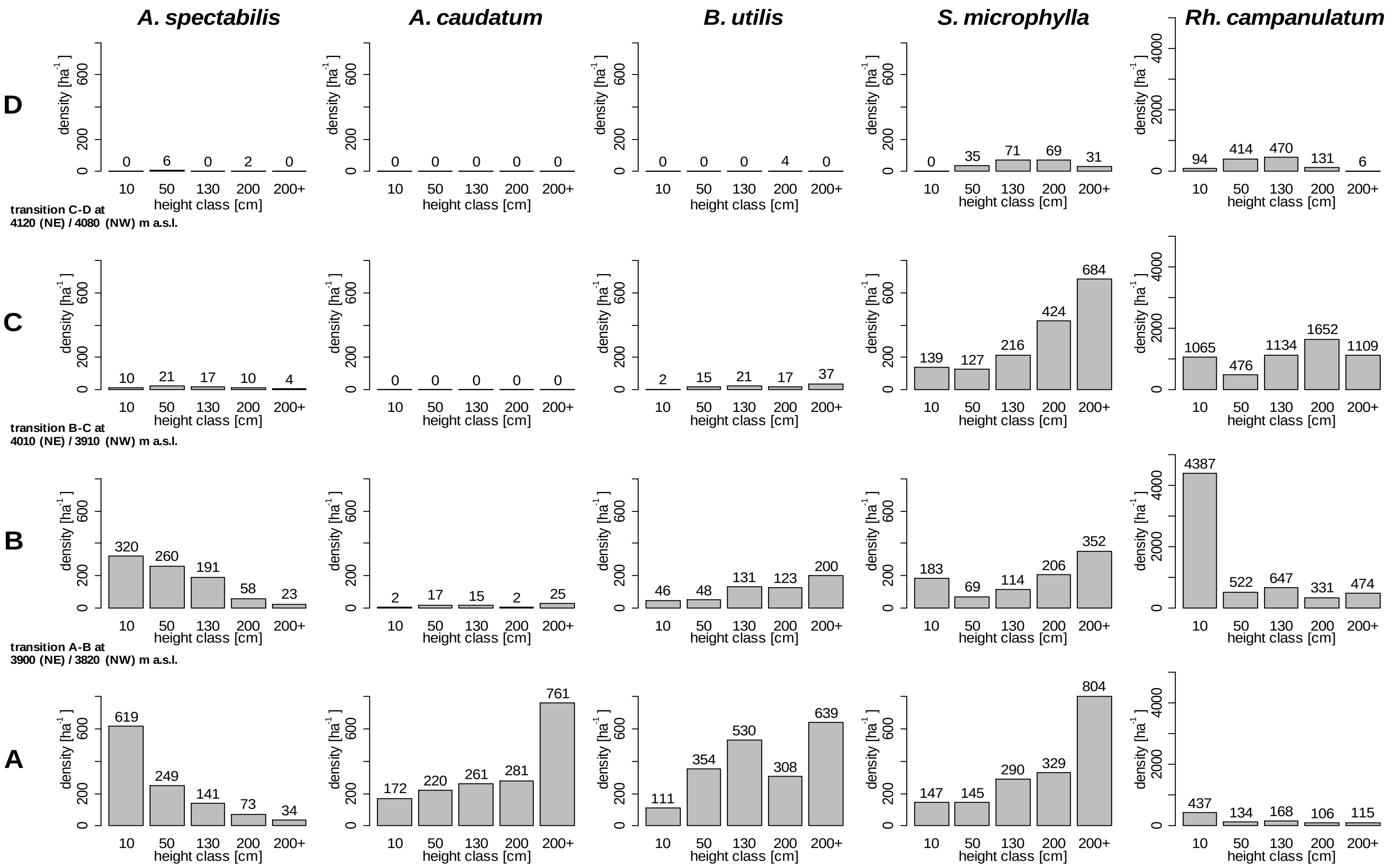

Fig. 16.8 Species-wise recruit (< 7 cm dbh) height class distribution of the most abundant tree species in the altitudinal zones A, B, C and D. Height class intervals: 10: ≤ 10 cm, 50: ≤ 50 cm, 130: ≤ 130 cm, 200: ≤ 200 cm, 200+: > 200 cm. Note difference in scaling of *Rh. campanulatum* y-axis (Source: Niels Schwab)

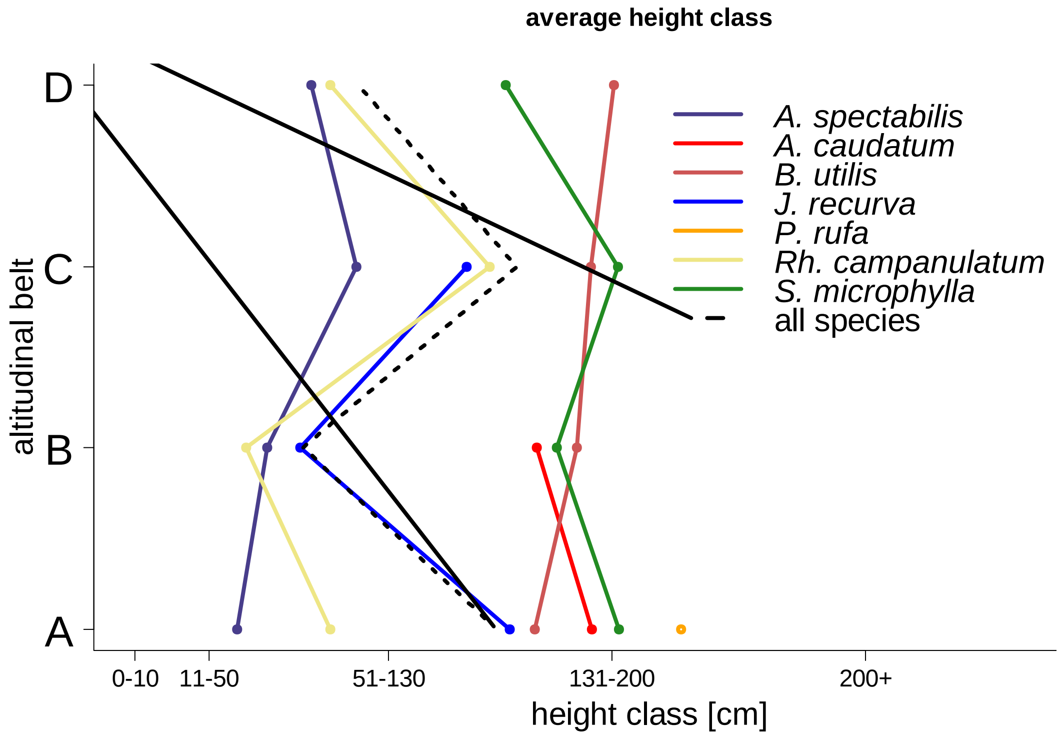

Fig. 16.9 Recruit height class distribution along the altitudinal gradient for all species and species wise (Source: Niels Schwab)

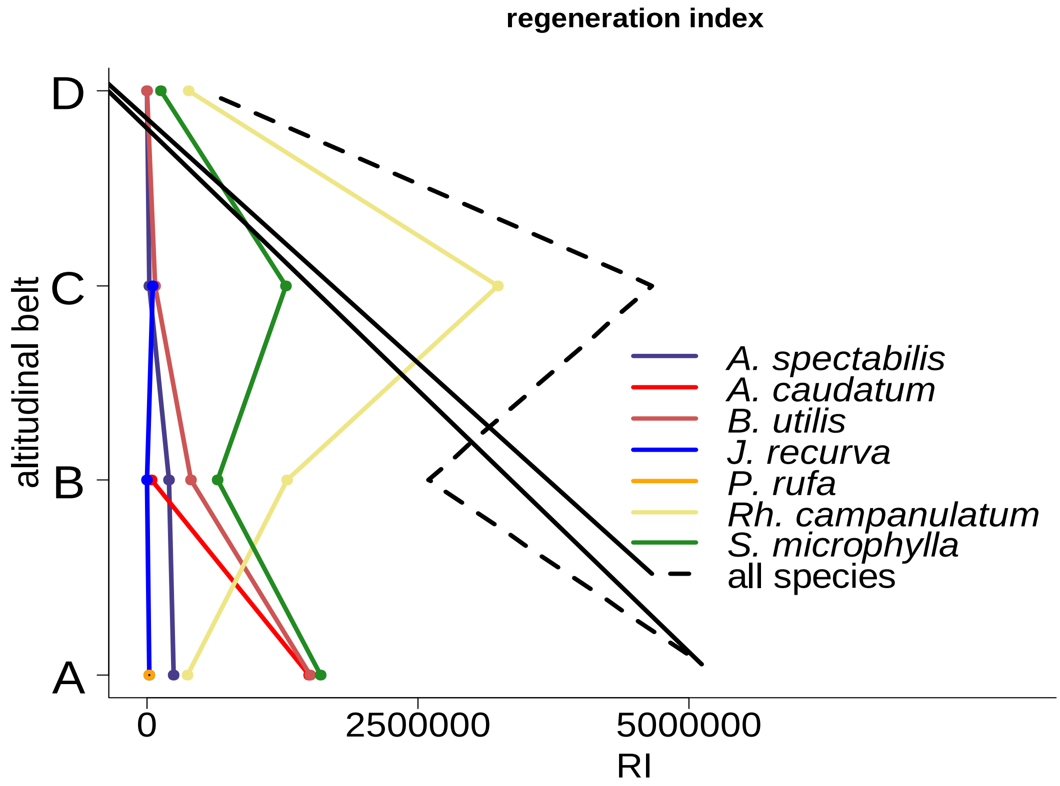

Fig. 16.10 Regeneration index *RI* species wise and sum of all species (Source: Niels Schwab)

16.3.5 Abruptness Patterns of Trees and Recruits at Elevational Transitions

In general, values of stand parameters such as dbh, tree height, and tree density decreased with elevation. Along this gradient, the degree of abruptness of these parameters increased at the transitions between single zones (Fig. 16.11, Tables 16.4 and 16.5). The abruptness of recruit density exhibited the same trend while the abruptness in terms of recruit height classes was highest at the transition A to B, lowest at B to C, and intermediate at the transition from zone C to D (Fig. 16.11, Tables 16.4 and 16.5).

The total all-species tree density (Table 16.4, Fig. 16.11) decreased most abruptly (abruptness = 0.96) at the transition CD, while the decrease was less but nearly equally abrupt for dbh and tree height at BC and CD (dbh: abruptness = 0.48 resp. 0.52; height: abruptness = 0.39 resp. 0.45). This pattern differed between single species: Density of *B. utilis, S. microphylla* and to a certain extent *A. spectabilis* trees decreased abruptly at the transition from B to C (abruptness = 0.92 resp. 0.62 resp. 0.5) while *Rh. campanulatum*'s density increased intermediately from B to C (abruptness= -0.32) and dropped abruptly from maximum to the smallest density at the transition from C to D (abruptness = 1). Abruptness of the transitions with regard to dbh and tree height did not resemble density abruptness, neither for all species nor species-wise (Table 16.4). For instance, *B. utilis*, *Rh. campanulatum* and *A. spectabilis* showed the most abrupt transitions in tree height at CD and this applied also for dbh of *B. utilis* and *Rh. campanulatum*. The majority of transitions of all species' trees showed positive abruptness values, indicating the decrease of dbh, height and stand density with elevation. Negative values mainly occurred at the transition from zone A to B, e.g. for all species density (intermediate, abruptness = -0.34), densities of *B. utilis* (smooth, abruptness = -0.21) and *Rh. campanulatum* (abrupt, abruptness = -0.54) and dbh of *A. spectabilis* (abrupt, abruptness = -0.53). While we found uniform numbers of abrupt and smooth transitions for trees of *A. spectabilis, B. utilis* and *Rh. campanulatum,* the smooth transitions nearly doubled the number of abrupt ones in case of *S. microphylla*.

The total all-species recruit density (Table 16.5, Fig. 16.11) decreased most abruptly (abruptness = 0.8) at the transition from zone C to D while there were distinct decreases in terms of recruit height at the transitions from zone A to B (abrupt, abruptness = 0.57) and from C to D (intermediate, abruptness = 0.41). As for trees this all-species pattern was not resembled by every single species: Density of *Rh. campanulatum* and *S. microphylla* recruits decreased abruptly at the transition from zone C to D (abruptness = 0.8 resp. abruptness = 0.92) while the most abrupt decreases of *A. spectabilis* and *B. utilis* recruits occurred at the transition BC (abruptness = 0.72) and AB (abruptness = 0.72) respectively. Again, abruptness of the transitions with regard to recruits' height did not resemble density abruptness neither for all species nor species-wise (Table 16.5). In general, we found many negative values, indicating increasing recruit heights with elevation. *Rh. campanulatum, S. microphylla* and *A. spectabilis* recruits' mean height increased abruptly at the transition from zone B to C (abruptness = -1.0 resp. abruptness = -0.88 resp. abruptness = -0.68). Except *B. utilis*, which showed increasing recruit height at all transitions, decreasing recruit heights at the transition from zone C to D were found. These were smooth for *A. spectabilis* (abruptness = 0.16), intermediate for *Rh. campanulatum* (abruptness = 0.43) and abrupt for *S. microphylla* (abruptness = 1.0).

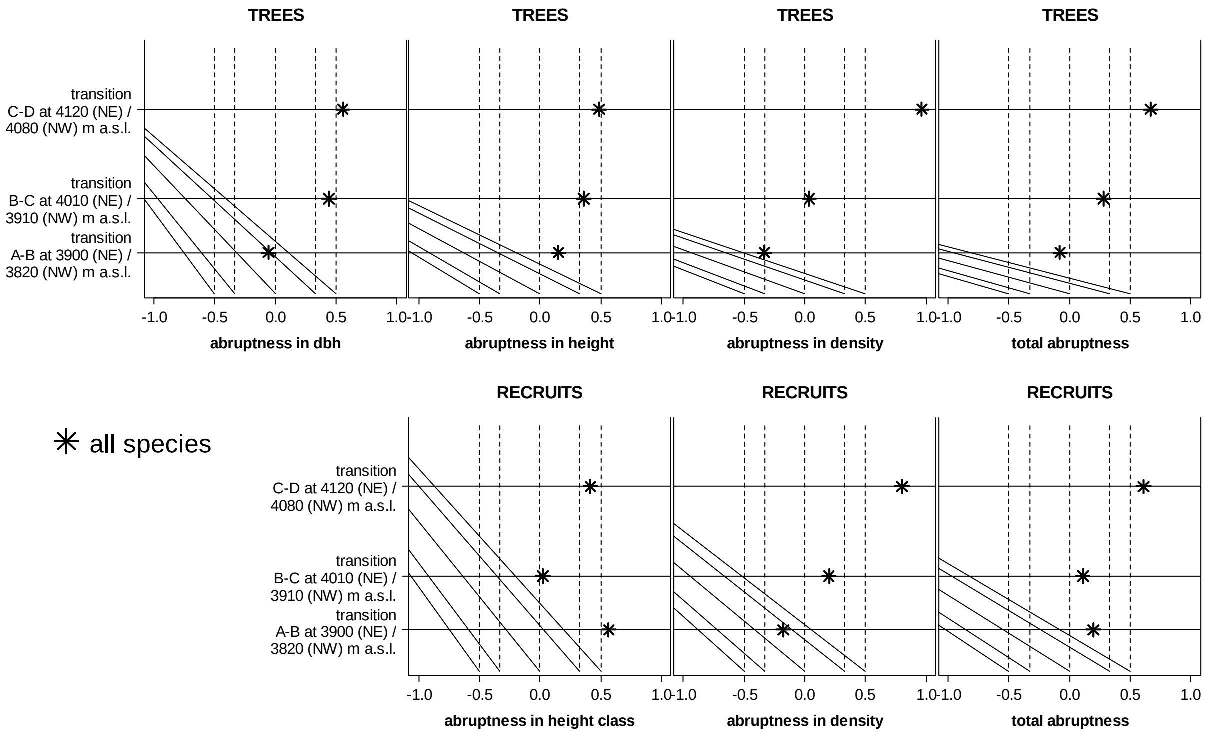

Fig. 16.11 Abruptness in dbh, height, density and sum of abruptness values for trees and recruits from zone A to B, B to C and C to D (Source: Niels Schwab)

Table 16.4 Abruptness of transitions of tree (dbh ≥ 7 cm) densities, dbh and height for all species and species-wise

	all species			***A. spectabilis***			***A. caudatum***			***B. utilis***			***P. rufa***			***Rh. campanulatum***			***S. microphylla***		
	density	dbh	height	density	dbh	height	density	dbh	height	density	dbh	height	density	dbh	height	density	dbh	height	density	dbh	height
CD	0.96	0.52	0.45	0.03	0.44	0.65	0.00	0.00	0.00	0.08	0.70	0.76	0.00	0.00	0.00	1.00	0.78	0.60	0.14	0.38	0.18
BC	0.04	0.48	0.39	0.50	0.56	0.35	0.00	0.00	0.00	0.92	0.26	0.22	0.44	1.00	0.90	-0.32	0.18	0.33	0.61	0.30	0.65
AB	-0.34	-0.06	0.16	0.47	-0.53	-0.28	1.00	1.00	1.00	-0.21	0.04	0.02	0.56	-0.14	0.10	-0.54	0.05	0.07	0.24	0.32	0.17

Table 16.5 Abruptness of transitions of recruit (dbh < 7 cm) density and height for all species and species-wise

	all species		***A. spectabilis***		***A. caudatum***		***B. utilis***		***J. recurva***		***P. rufa***		***Rh. campanulatum***		***S. microphylla***	
	density	height cl.	density	height cl.	density	height cl.	density	height cl.	density	height cl.	density	height cl.	density	height cl.	density	height cl.
CD	0.80	0.41	0.05	0.16	0.00	0.00	0.05	-0.43	1.00	0.96	0.00	0.00	0.80	0.43	0.92	1.00
BC	0.20	0.02	0.72	-0.68	0.04	0.94	0.24	-0.20	-0.96	-0.23	0.00	0.00	0.17	-1.00	-0.44	-0.88
AB	-0.18	0.57	0.24	-0.32	0.96	0.06	0.72	-0.37	0.17	0.27	1.00	1.00	-1.00	0.37	0.52	0.88

16.3.6 Near-Natural State of Treeline Ecotone

All assessed density-diameter distributions resembled a reverse J- or L-shape, thus indicating a near-natural state of the Rolwaling treeline. The total number of tree stumps decreased considerably with elevation (Table 16.6). In zone B, the basal area of stumps (medium and less decomposition) amounted only to 3 % of the total basal area (living trees and stumps), while it was less than 0.5 % in zone C. Thus, wood cutting and its influence on stand structures is negligible. In zone A, the stump basal area was higher (21 %), but potential modifications of stand structure here do not affect timberline and treeline transitions at higher altitudes. The species composition of stumps of all decomposition classes exhibited *S. microphylla* (c. 17 stumps per plot in average), *A. caudatum* (c. 11) and *B. utilis* (c. 9) as most affected in zone A. *S. microphylla* (c. 7), *Rh. campanulatum* (c. 7) and *B. utilis* (c. 6) accounted for most stumps in zone B (Table 16.6).

According to our field observations influences of herbivores and domesticated animals can be ruled out. We found minimal evidence for deer, like faeces and bark stripping. We observed pika (*Ochotona* sp.), weasel (*Mustela* sp.) and snowcock (*Tetraogallus* sp.) more often, but no influence on treeline stand structures could be identified. Since the study slopes are separated by the river from settlements and thus very difficult to access, we did not observe any grazing impact. Further evidence for a negligible anthropogenic impact in the Rolwaling treeline ecotone is given by soil and atmospheric data. Investigations of bulk densities in the prevailing Podzol soils revealed low mean values from 0.01 g cm^{-3} (decomposition layer) to a maximum of 1.14 g cm^{-3} (Ae horizons), indicating obviously undisturbed soils. Monitoring of atmospheric nitrogen deposition (nitrogen dioxide (NO_2), ammonia (NH_3)) below detection limit indicate no effect in the study area.

Table 16.6 Mean basal area of tree stumps (≥ 7 cm diameter) in proportion to stump + living trees (≥ 7cm dbh) mean basal area in altitudinal zones A, B, C, and D (in total and differentiated in causes of death), and species composition of stumps.

condition		**A**	**B**	**C**	**D**
living trees	basal area trees [m²/ha]	28.77	47.93	13.29	0.01
undecomposed + slight decomposition	**stumps basal area (total basal area of living trees + stumps = 100%) [%]**	**7.1**	**0.04**	**0.08**	**0.00**
	natural cause [%]	0.00	43.36	0.00	-
	anthropogenic cause [%]	93.71	56.64	0.00	-
	unidentified cause [%]	6.29	0.00	100.00	-
undecomposed + slight + medium decomposition	**stumps basal area (total basal area of living trees + stumps = 100%) [%]**	**19.04**	**2.89**	**0.49**	**0.00**
	natural cause [%]	0.00	0.56	0.00	-
	anthropogenic cause [%]	96.13	90.94	20.20	-
	unidentified cause [%]	3.87	8.50	79.80	-
undecomposed + slight + medium + intense decomposition	**stumps basal area (total basal area of living trees + stumps = 100%) [%]**	**64.65**	**20.81**	**5.15**	**0.00**
	natural cause [%]	0.17	28.56	35.63	-
	anthropogenic cause [%]	51.29	31.57	32.68	-
	unidentified cause [%]	48.54	39.87	31.69	-

species composition of stumps

	mean number of stumps per plot	**A**	**B**	**C**	**D**
all decomposition classes	*Abies spectabilis*	6.00	1.86	0.00	0.00
	Acer caudatum	11.00	0.00	0.00	0.00
	Betula utilis	9.00	5.67	2.50	0.00
	Prunus rufa	1.67	0.00	0.00	0.00
	Rhododendron campanulatum	3.00	6.67	4.00	0.00
	Sorbus microphylla	16.62	6.60	3.00	0.00
	unidentified	9.00	5.00	0.00	0.00
	sum	**56.28**	**25.79**	**9.50**	**0.00**

16.3.7 Soil and Air Temperatures

In general, mean soil and mean air temperatures show similarly decreasing trends with elevation (Fig. 16.12). In winter (DJF) and autumn (ON) seasons of 2013, the mean soil temperatures of zones B and D exceeded soil temperatures of the respective subjacent zones, most likely due to cold air drainage (A) and less irradiation and/or less snow cover insulation (evergreen *Rh. campanulatum* cover in zone C). We measured a growing season mean soil temperature of 7.5 ± 0.5°C at the transition from zone B to C. Growing degree days differed between the two lower zones (A: 175 days, B: 177 days) and the upper zones (C: 158 days, D: 154 days) showing a shortening of the growing season in the uppermost zones by c. three weeks.

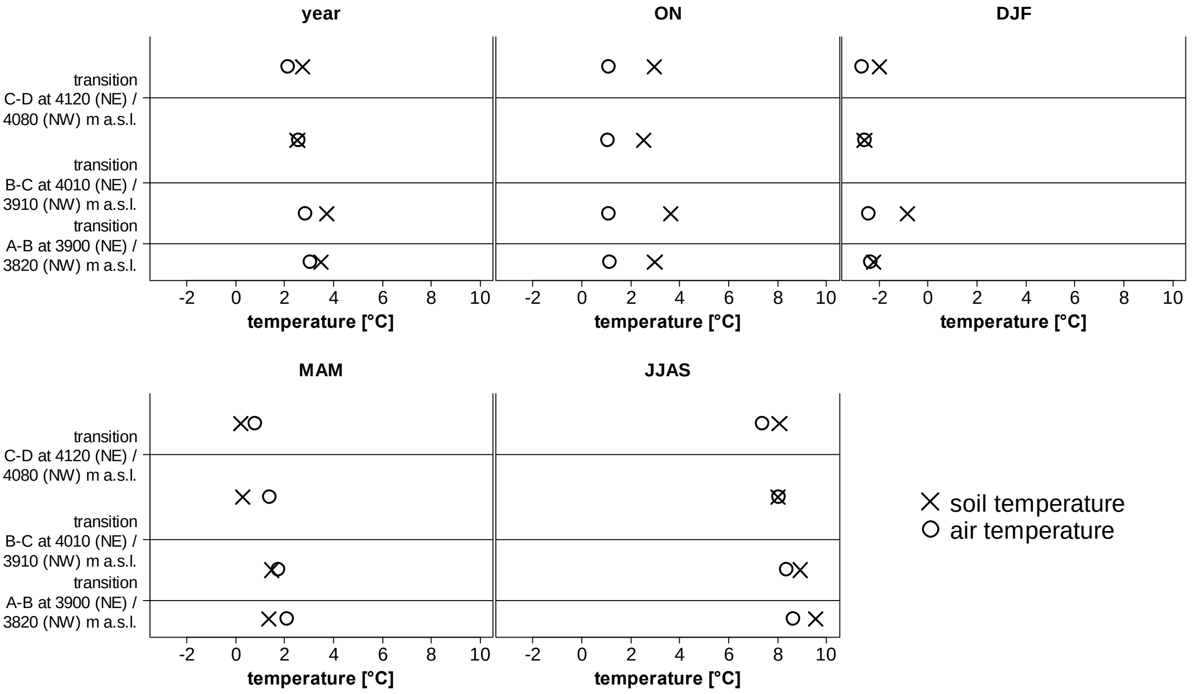

Fig. 16.12 Yearly and seasons' mean soil and air temperatures of the four altitudinal zones *A*, *B*, *C* and *D*. *ON* October/November, *DJF* December-February, *MAM* March-May, *JJAS* June-September (Source: Niels Schwab)

Yearly mean soil and air temperatures differed most in altitudinal zone B (soil: 3.7°C; air: 2.8°C) and nearly equalled in zone C (soil: 2.5°C; air: 2.6°C). At BC, the transitions of soil temperature (zone B → zone C; year: -1.2°C; ON: -1.1°C; DJF: -1.8°C; MAM: -1.2°C; JJAS: -0.9°C) exceeded the differences of air temperatures (zone B → zone C; year: -0.3°C; ON: -0.1°C; DJF: -0.1°C; MAM: -0.4°C; JJAS: -0.3°C). Soil temperatures exhibited abrupt transitions along the elevational gradient (Fig. 16.13). The annual mean soil temperature and mean soil temperatures of autumn, winter (all abruptness = 1) and spring (abruptness = 0.94) dropped very abruptly at the transition BC. This decrease was less pronounced in summer (abruptness = 0.59). We found rather unexpected increases of soil temperatures with increasing elevation at the AB and CD transitions in autumn (abruptness = -0.59 resp. abruptness = -0.39), winter (abruptness = -0.78 resp. abruptness = -0.34), and for the annual mean soil temperatures (abruptness = -0.22 resp. abruptness = -0.18). In spring, the soil temperatures of the transitions AB (abruptness = -0.08), and CD (abruptness = 0.06) were similar to each other. In summer, soil temperatures decreased nearly abruptly from zone A to

B (abruptness = 0.41), while they differed only slightly at the transition from zone C to D (abruptness = -0.03).

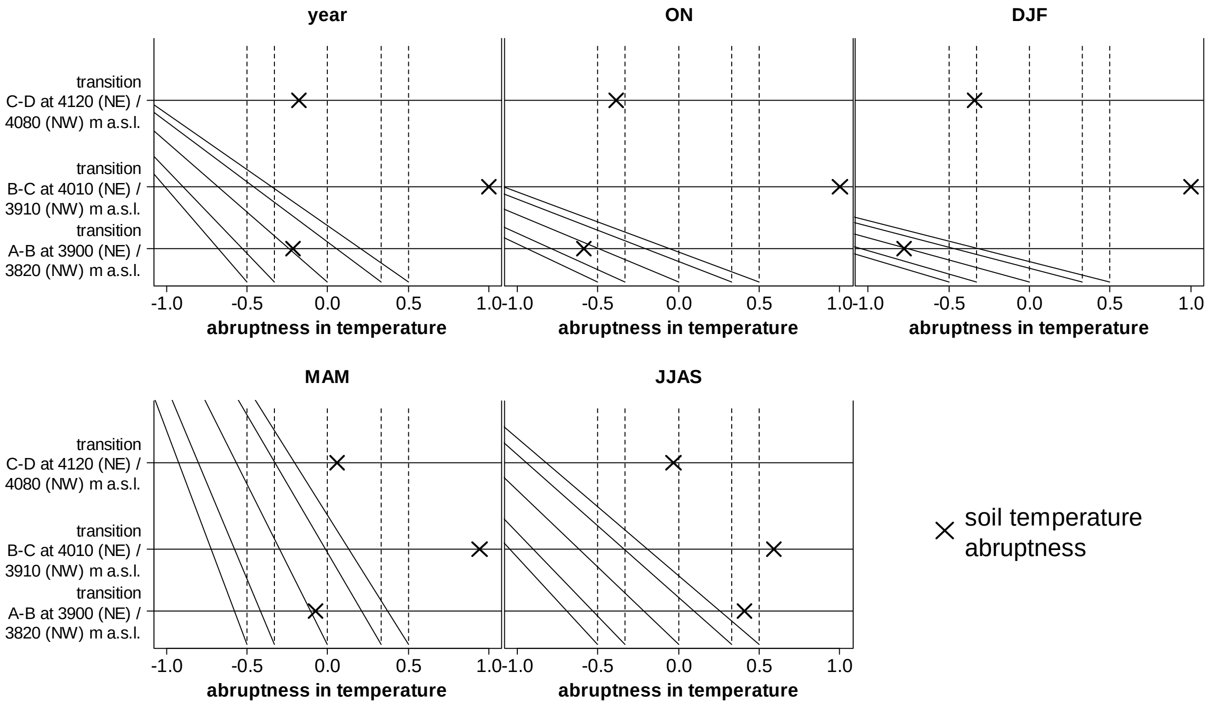

Fig. 16.13 Yearly and seasons' mean soil temperature abruptness along the altitudinal gradient at transitions from zone *A* to *B*, *B* to *C* and *C* to *D*. *ON* October/November, *DJF* December-February, *MAM* March-May, *JJAS* June-September (Source: Niels Schwab)

16.4 Discussion

16.4.1 Treeline Structure and Treeline Responsiveness to Climate Warming

In general, the tree species composition and altitudinal position of the Rolwaling treeline ecotone coincides with previous findings for north-facing slopes in central and E Nepal, where *A. spectabilis*, *B. utilis, S. microphylla* and *Rh. campanulatum* dominate the ecotones between 3900 and 4400 m (Schickhoff 2005; Miehe et al. 2015). Considering the altitudinal zonation of vegetation within the treeline ecotone, in particular the dense *Rh. campanulatum* thicket in zone C, it is evident that the Rolwaling treeline has to be assigned physiognomically to treelines with a krummholz belt (cf. Holtmeier 2009). The contorted and gnarled growth form of *Rh. campanulatum* is, however, not necessarily genetically pre-determined (cf. Miehe 1990), since there are some upright-growing individuals at lower altitudes in zones A and B

(Fig. 16.14). *Rh. campanulatum* thickets in the lower C zone reach a considerable height of more than 3-4 meters and stems may attain large diameters. Thus, these thickets can also be termed dwarf forests (cf. Masuzawa 1985). Towards their upper altitudinal limit at the transition CD, these thickets or dwarf forests are gradually reduced in height and become climatically stunted. Within the krummholz thicket in lower zone C, the uppermost tree individuals (> 3 m height) of *A. spectabilis* and *B. utilis* mark the outpost-treeline sensu Körner (2012, Fig. 16.3), which is located slightly upslope (30-50 m altitude difference) from the treeline. The latter connects the uppermost patches of forest composed of trees with true tree habitus, and coincides with the transition BC (4010 m NE; 3910 m NW) in our slope stratification scheme (cf. Fig. 16.1 and 16.2). Within the subalpine forest, *Abies* and *Betula* trees reach timber size up to the treeline, thus the difference in altitude between timberline and treeline is negligible (terminology sensu Körner 2012).

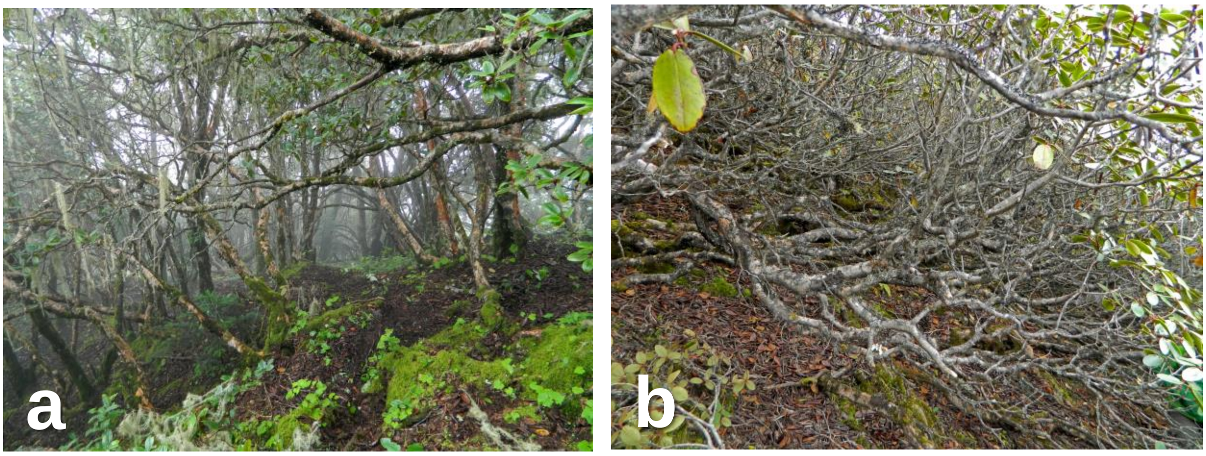

Fig. 16.14 *Rh. campanulatum* growing upright in zones A and B (**a**) and as krummholz in zone C (**b**) (Source: Niels Schwab; a: 30 July 2013, b: 29 September 2014)

Variations in uppermost distribution limits of treeline species basically reflect species-specific physiological capacities to survive environmental stresses. Limits on upslope expansion can be imposed by potentially limiting resources (carbon, water, nutrients) and by physical factors, for instance growing season length, frost intensity, wind exposure, abrasion, etc. (Crawford 2008). Obviously, physiological tolerances of treeline species in Rolwaling are sufficient to establish recruits far above the uppermost adult trees. The wide krummholz belt (up to 200 m altitude difference) with absolute dominance of *Rh. campanulatum* does not constitute an insurmountable barrier for other treeline species. Uppermost individuals of *A. spectabilis* (4185 m), *B. utilis* (4140 m), and *S. microphylla* (4245 m) occur above the krummholz belt in zone D. The tree species lines give evidence of successful regeneration even under the harsh climatic conditions of treeless terrain, at least to a sapling stage of 1-2 m height. Although these recruits are few in number, mostly stunted, mostly growing in the 'chamaephyte environment' (Wieser et al. 2014), and far away from reaching any tree size definition, they partially project above the snow cover, and indicate the potential for treeline advance under more favourable environmental conditions. Even above the krummholz belt tree species might be hindered by the dense alpine dwarf scrub heath vegetation (mainly composed of *Rh. anthopogon*, *Rh. lepidotum*, *Rh. setosum*) because shrub community competitive abilities might affect tree establishment (Körner 2012; Schickhoff et al. 2015, 2016; Chhetri and Cairns 2015). The recruit density of *A. spectabilis* decreases abruptly from B to C. The abrupt decrease indicates a lower potential for upward migration in comparison to *B. utilis* recruits which showed a smooth transition in density and height from B to C. *S. microphylla* has the best premise to advance to higher elevations given the negative abruptness values of *Sorbus* recruits at the transition from zone B to C and absolute density and mean height values.

How is the structure of the Rolwaling treeline related to the responsiveness to climate warming? Our data suggests that the extensive *Rh. campanulatum* krummholz belt plays a crucial role for any treeline shift to higher altitudes. High competitiveness and absolute dominance of *Rh. campanulatum* prohibits to a large extent upslope migration of other treeline tree species from the closed forests in zones A and B. Supposed allelopathic effects of *Rh. campanulatum* might contribute to the low establishment rates of other tree species in the krummholz thickets (Schickhoff et al. 2015, 2016). Thus, 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). Our results are in line with Harsch and Bader (2011), who concluded from a global treeline dataset a comparatively low responsiveness of krummholz treelines compared to diffuse treelines. They found the majority of diffuse treelines and only one third of krummholz treelines to be advancing, while abrupt and island treelines were found to be rather stable. The disjunction of mechanisms and environmental conditions primarily associated with these different treeline forms seem to explain this pattern (cf. Harsch and Bader 2011). Krummholz treelines in the Himalaya (cf. Miehe 1990, 1991; Schmidt-Vogt 1990; Miehe and Miehe 2000) have not been analyzed so far with regard to their responsiveness to climate warming. Schickhoff et al. (2015) provide a first overview of the sensitivity of krummholz treelines in Rolwaling and Langtang. In the latter, seedling establishment beyond the actual upper limit of contiguous forests was detected which is a sign for a potential treeline shift. Chhetri and Cairns (2015) found a slight upward shift of an undisturbed diffuse treeline in Nepals Makalu Barun National Park. However, they state that the treeline has advanced only until the early 20th century. Other studies on treelines in Nepal Himalaya report tree and/or recruit densities of all occurring or selected species (Ghimire and Lekhak 2007; Shrestha et al. 2007; Gaire et al. 2010; Ghimire et al. 2010; Gaire et al. 2011; Lv and Zhang 2012; Sujakhu et al. 2013; Gaire et al. 2014; Shrestha et al. 2014). None of the cited studies refers to a treeline ecotone which is regarding dominance and spatial extent similar to zone C of our study area. In general, most treeline ecotones in Nepal are disturbed by human impact which has changed population structures since long.

Our data suggest that high abruptness values along the altitudinal gradient are associated with major changes in site factors. At the transition BC, i.e. the transition from upright-growing tree individuals to krummholz, we found the most abrupt change in soil temperatures. The distinct decrease in soil temperatures is obviously related to the dense foliage and canopy of the evergreen *Rh. campanulatum* thickets which provide a more efficient isolation of the soil surface from solar radiation and subsequent heat transformation compared to the upper subalpine *Abies-Betula* forest. Abrupt microenvironmental changes are commonly associated with abrupt treelines (cf. Harsch and Bader 2011; Cieraad and McGlone 2014), corresponding in the Rolwaling case to an abrupt transition from forest to krummholz. Although krummholz treelines represent a definite treeline form they can obviously feature abrupt treeline characteristics (cf. Fig. 16.2).

In contrast to diffuse treelines, advances of both, abrupt and krummholz treelines are connected rather to winter warming and reduced winter stress factors than to growing season temperature (Harsch et al. 2009). Tree growth is assumed being rather limited by dieback (short-term stressors) than by limited biomass gain (long-term mild stress, Harsch and Bader 2011). In consequence, it is likely that the Rolwaling treeline is rather influenced by winter condition stress factors. These lead to plant damage and limit survival. Vertical growth in krummholz depends on the degree of structural microsite facilitation, e.g. reduced wind and sun exposure and beyond treeline tall seedling growth is likely limited by the same factors (Smith et al. 2003). Thus, recruitment beyond treeline is restricted as long as vertical growth limiting conditions prevail (Harsch et al. 2009). In Rolwaling, growing season temperature and length is likely to increase while duration of winter conditions (frost days) decreases (Gerlitz et al. 2014). Nevertheless, we assume that the consequences of winter conditions for plant growth will not change substantially because processes like for instance wind abrasion, snow and ice damage occur regardless of the length of the frost period. Most likely heavy snowpack provokes mechanical stress and dieback in the krummholz belt. A short-term treeline shift in response to climate warming is not to be expected.

Obviously, *Rh. campanulatum* wood has mechanical properties which enable the described growth form, similar to the flexibility of e.g., *Alnus* sp., *Betula* sp., *Salix* sp. and *Nothofagus* sp. at various treelines on earth (Jalkanen and Konocpka 1998; Gallenmüller et al. 1999; Körner 2012). Most likely, this property facilitates the establishment of *Rh. campanulatum* under harsh climatic conditions.

B. utilis, and to a lesser extent *A. spectabilis* and *S. microphylla,* shows maximum abruptness values over different transitions (Tables 16.4 and 16.5). This distribution indicates that these species still perform well in growth parameters like dbh and tree height in zone C, while density decreases abruptly at lower altitude. Single individuals of *A. spectabilis, B. utilis,* and *S. microphylla* appear to profit from variations in *Rh. campanulatum* density (canopy openings) and/or variations in environmental factors like e.g., exposition and soil parameters (micro-site facilitation). The abruptness values of the Rolwaling treeline ecotone show a heterogeneous pattern across slopes and development stages (Tables 16.4 and 16.5 and Fig.

16.15) confirming the need for a differentiated categorization and species-specific analyses of treelines at local and landscape scales (Trant and Hermanutz 2014; Schickhoff et al. 2015, 2016).

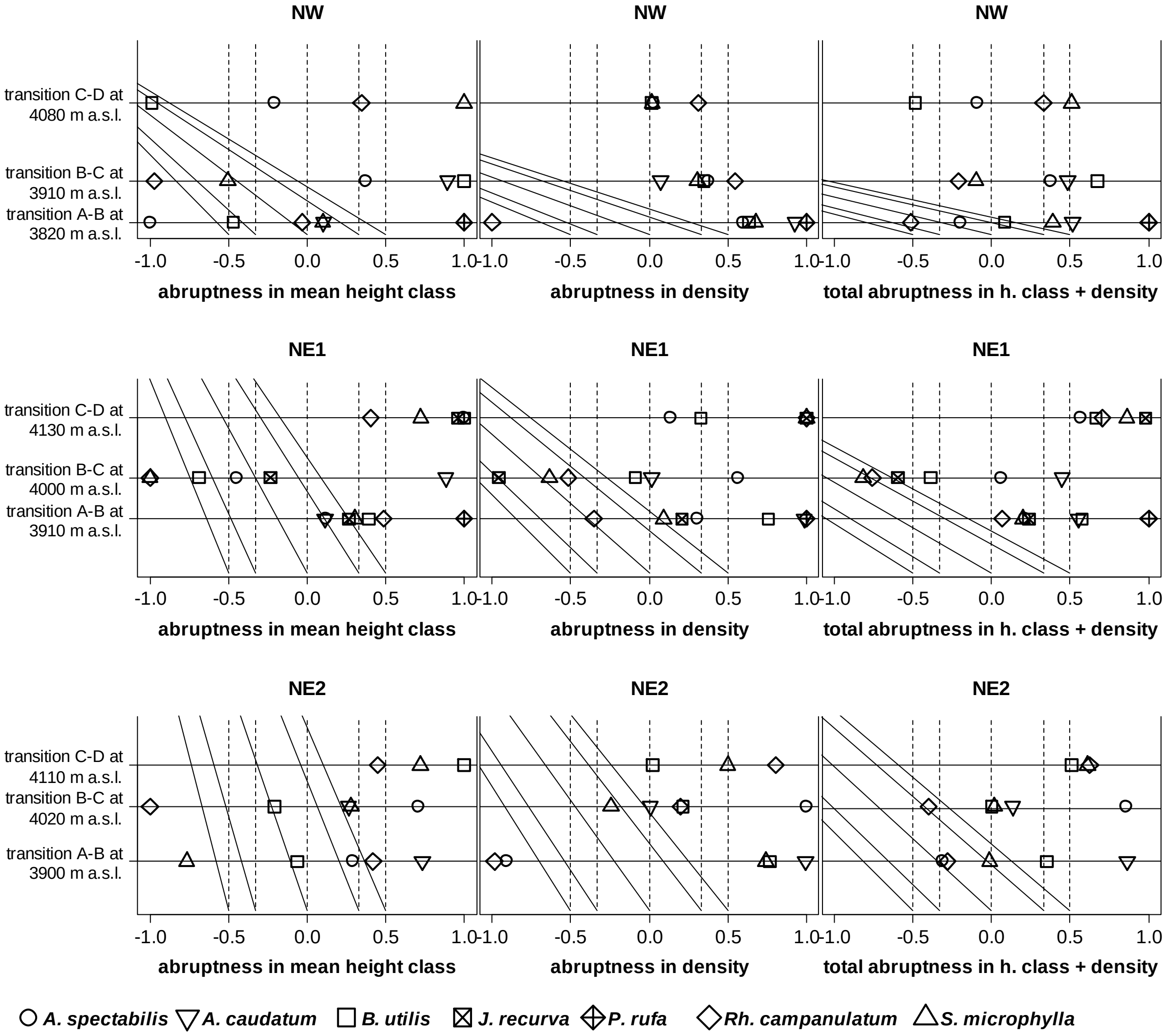

Fig. 16.15 Species- and slope-wise height, density and total recruit abruptness of transitions from zone *A* to *B*, *B* to *C* and *C* to *D* (Source: Niels Schwab)

16.4.2 Soil Temperature and Regeneration

In general, tree and recruit species compositions of altitudinal zones correspond to each other with distinct higher number of recruits than trees (Figs. 16.4, 16.5 and 16.6), indicating sustainable regeneration and stable populations. However, no tree individual of any species occurred in Zone D (except *S. microphylla*), while recruits of *A. spectabilis*, *B. utilis*, *S. microphylla* and *Rh. campanulatum* exist. These recruits are potential indicators for an upward shift of tree species distributions triggered by recent climate warming (see above), and a recent increase in recruit density could increase the numbers of trees in the near future. The occurrence of recruits in zone D indicates the potential of tree species to become established above the krummholz belt.

Recruit densities of *A. spectabilis*, *B. utilis*, and *S. microphylla* correlate positively in nearly all height classes with soil temperature. *Rh. campanulatum* densities correlate both, positively (height classes < 3 cm and > 200cm) and negatively (height ≥ 3 cm and ≤ 200cm; cf. Schickhoff et al. 2015). Thus, increasing soil temperatures potentially support the process of tree species establishment above the current treeline. Interestingly, soil temperatures at the Rolwaling treeline are higher compared to the global mean at treeline elevations. We measured a growing season mean soil temperature of 7.5 ± 0.5°C under uppermost forest stands of *A. spectabilis* and *B. utilis* at the transition BC (Müller et al. 2016), a similar value as the warm temperate bioclimatic region seasonal mean temperature of 7.4 ± 0.4°C, but distinctly higher than the global growing season mean soil temperature of 6.4 ± 0.7°C (Körner 2012). This significant deviation from the global mean adds to the rather broad range of soil temperatures (5-9°C) measured at treeline elevations (e.g. Walter and Medina 1969; Winiger 1981; Bernoulli and Körner 1999; Körner and Paulsen 2004; Gehrig-Fasel et al. 2008; Shi et al. 2008; Hoch and Körner 2009; Kessler et al. 2014), and suggests a broadening rather than a narrowing of the error term of ± 0.7°C postulated by Körner (2012). In terms of soil temperatures, the Rolwaling treeline appears to be decoupled from rapid climate warming, i.e. the above-average soil temperatures might imply a retarded tracking of climate warming and a decelerated shift of treeline position (cf. Müller et al. 2016).

The more linear trend of air temperatures and in comparison to soil temperatures less pronounced differences between zone B and C can be attributed to the statistical method used to obtain these values (Gerlitz et al. 2016), while the soil temperatures were measured directly on site. However, heat deficiency above the subalpine forests is caused by a combination of low soil and air temperatures.

Above-average soil temperatures as well as an increasing number of growing degree days (representative for the Himalayan south slope; cf. Shrestha et al. 2012; Gerlitz et al. 2014) set the stage for an upward migration of tree species. We assume the current treeline to be located below its potential climatic limit. Since the ecotone is not affected by land use, the treeline is obviously suppressed by the given constellation of environmental factors (e.g., soil nutrient availability, krummholz barrier, allelopathic effects) and of facilitative (positive) resp. competitive (negative) interactions of recruits with neighbouring vegetation. The high numbers of *S. microphylla* recruits above the treeline (= in zones C and D) might result from a recent upward migration resp. stand densification, and if so, support the view of a species-specific response to climate change. Rather *S. microphylla* recruits than those of other tree species are capable to overcome the permanently densely foliated and potentially allelopathic krummholz belt.

16.4.3 Species-Specific Regeneration

In general, the results of our regeneration studies which show reverse J-shaped density diameter distributions, and indicate intense and sustainable regeneration and thus the potential for upward migrations, are in line with other studies from treelines in Nepal (e.g. Ghimire and Lekhak 2007; Shrestha et al. 2007; Gaire et al. 2010; Ghimire et al. 2010; Gaire et al. 2011; Sujakhu et al. 2013; Gaire et al. 2014). In some of the J-shapes of these studies the smallest dbh class is not included (Ghimire and Lekhak 2007; Shrestha et al. 2007), or shows smaller numbers than the subsequent class (Gaire et al. 2010; Gaire et al. 2011; Sujakhu et al. 2013; Gaire et al. 2014) putting their statements regarding intense and sustainable regeneration into a different perspective. Low numbers in the small dbh class indicate grazing impact by domesticated or wild animals, which exacerbate the interpretation of the results regarding migration potentials. The species-specific low numbers in the tallest diameter classes or absence of classes above 50 cm dbh in some studies (Ghimire and Lekhak 2007, Gaire et al. 2010; Gaire et al. 2011; Sujakhu et al. 2013; Gaire et al. 2014) are signs indicating anthropogenic impacts. Some studies (Lv and Zhang 2012; Gaire et al. 2014) detected rather bell-shaped density-diameter distributions or reverse J-shaped distributions (Gaire et al. 2010; Gaire et al. 2011; Sujakhu et al. 2013; Gaire et al. 2014) that do not correspond to the reverse J- or L-shaped ones we found in Rolwaling being to a much higher degree dominated by recruits. However, Gaire et al. (2014) assessed a significant upward shift, densification and high recruitment intensity of *A. spectabilis* at their study site in Manaslu Conservation Area. Even in this study the low dbh classes show only small numbers of recruits, especially in case of *B. utilis*. In our study area, zone A provides a much better basis for regeneration of *A. spectabilis, B. utilis* and *S. microphylla* compared to zone B, where their recruit numbers are distinctly lower compared to tree densities (Figs. 16.4, 16.5 and 16.6). The reason might be competitive advantages of *Rh. campanulatum* in zone B. However, the competitive strength of *Rh. campanulatum* seems to be strongest in zone C. This applies especially for the taller individuals (≥ 7 cm dbh).

Few studies from Nepal provide data on recruit densities. In Langtang valley, Gaire et al. (2010; 2011) found significantly less *B. utilis* recruits per ha, about the same number of *A. spectabilis* and significantly less *Rh. campanulatum* and *S. microphylla* recruits compared to the ecotone in Rolwaling. In comparison to our results, Schickhoff et al. (2015) found a comparable distribution of seedling and sapling species and slightly higher total numbers of recruits in Langtang. *Pinus wallichiana* recruit density was very high (c. 4500 N/ha at lower altitude; c. 1000 N/ha at higher altitude) in Manang (Ghimire et al. 2010), however the investigated forest was obviously dominated by this single species and thus showed a different species composition than the Rolwaling ecotone. In another study from Manang, *A. spectabilis* exhibited very high recruit numbers (c. 3200 N/ha). In the Manang study of Shrestha et al. (2007), *B. utilis* recruit numbers were comparable to the present study. In contrast, they found a very high number of *A. spectabilis* recruits at lower altitude (3500-3900 m a.s.l.; c. 5600 N/ha), while the number was distinctly smaller than ours at higher altitude

(3900-4200 m a.s.l.; c. 160 N/ha). *Pinus wallichiana* showed a similar pattern with high numbers at lower and smaller numbers at higher altitude. Recruit densities of *A. spectabilis* and *B. utilis* in Manaslu Conservation Area resembled roughly the corresponding densities in Rolwaling. In contrast, *Rh. campanulatum* recruits occurred only rarely (c. 200 N/ha, Sujakhu et al. 2013). *A. spectabilis* recruit numbers were smaller in Barun valley (c. 200 N/ha; Chhetri and Cairns 2015) compared to Rolwaling. In summary, several studies from Nepal report continuous regeneration and potentials for treeline shifts, consistent with our findings

In our study, the recruit height class distribution of *A. spectabilis* differs from *B. utilis*, *A. caudatum* and *S. microphylla*. Obviously, the latter species grow faster and aggregate more individuals in taller height classes. The height class patterns reflect inter alia varying reproduction strategies: We found vegetative propagation (coppices) for *B. utilis* and *S. microphylla* while *A. spectabilis* recruits grow separately from other individuals and sprout from seeds. As low temperatures restrict rather germination than layering (Holtmeier 2009; Wieser et al. 2014), temperatures obviously do not restrict seed based regeneration of *A. spectabilis* given the recruit height class and dbh distributions. The results of recruit mean height and RI show that *A. spectabilis* and *B. utilis* have the potential to develop above the transition BC beyond the seedling stage. The rare occurrence of trees indicates the potential to develop even further and become established. There are less *A. spectabilis* and *B. utilis* recruits in upper altitudinal zones, but the percentage of survivors that grow successfully to taller height classes is distinctly higher compared to lower elevation. Asynchronous shortages in seedling establishment in each zone at different time periods might be one reason for differing specifies- and altitudinal-specific patterns. Another reason could be that competitive stress is higher in the lower zones and thus a smaller percentage of recruits survive. More favourable light conditions appear to favour the growth of *B. utilis* in zone D and in openings in zone C. *S. microphylla* can be considered established in zones C and D given height class distribution and *RI*. Some species show no distinct signs of treeline shift but more obvious an intensified regeneration, indicating ongoing stand densification below treeline. This applies species-specific especially for *A. spectabilis* in zones A and B, *B. utilis* in zone A, *S. microphylla* in zone A and C and *Rh. campanulatum* in zones B to D where we found evidences for stand densification. Climate warming impact may influence regeneration below treeline and treeline shift in different intensities (e.g. Camarero and Gutiérrez 2004; Wang et al. 2006; Kirdyanov et al. 2012; Gaire et al. 2014; Shrestha et al. 2014) which seems to apply for our study area.

Rh. campanulatum's population structure in zones C and D is a sign for its potential to spread out further (cf. Figs. 16.4, 16.5, 16.6 and 16.8). In comparison to zones C and D, *Rh. campanulatum* seems to grow under more intense competitive stress in zone B. While the high *RI* and the very high number of recruits smaller than 10 cm height points to a viable regeneration, the very low mean height and relative small numbers of recruits in classes above 10 cm height imply competitive pressure by other species and a distinct self-thinning process. Obviously, *Rh. campanulatum* keeps its regeneration capacity in the zones above while the competitive strength of other species except *S. microphylla* seems to be reduced. As especially the *RI* of *S. microphylla* and also its average recruit height are relatively low in zone B, this species becomes more competitive in zones C and D. The shift in the ratio of recruits to trees at the specific tree species lines, recruit height and *RI* distributions indicate the potential for sustainable recruitment and tree growth. Positive correlations of recruit density with soil temperatures and soil moisture give evidence of the relevance of these site factors (cf. Schickhoff et al. 2015). However, other site factors such as nutrient availability, microclimatic variations, germination conditions like surface structure and light conditions might in addition hinder or facilitate intensified recruitment (e.g. Holtmeier and Broll 2005; Malanson et al. 2007; Hofgaard et al. 2009; Batllori et al. 2010; Holtmeier and Broll 2010; Renaud et al. 2011; Elliott 2012; Wang et al. 2012; Durak et al. 2015; Treml and Chuman 2015).

The high standard deviations of the mean densities which we present in the results reveal the heterogeneous patterns of the populations even within same altitudinal zones. Analyses of subsets of our sample e.g., single slopes confirm this finding. This applies also for general and species-specific abruptness patterns (e.g. recruits, species- and slope-wise, Fig. 16.15 and Tables 16.4 and 16.5). This variability suggests differences in site conditions apart from altitude, and thus a varied potential for recruitment at local scales. No distinct differences in soil temperatures between zone C and D were detected during growing season (Figs. 16.12 and 16.13). If dissemination depended on temperature only species which once establish in zone C could migrate easily to zone D as there is no temperature threshold to pass.

In summary we assessed a prolific regeneration in the Rolwaling treeline ecotone which indicates a considerable potential to respond to climate warming with a treeline shift. Any treeline advance, however, will be controlled to a large extent by the dense krummholz belt which acts as an effective barrier for upslope migration of treeline-forming tree species. Most likely the treeline in Rolwaling confirms the low responsiveness of near-natural Himalayan treelines and upward shifts only in the long term, despite the currently existing potential (Shrestha et al. 2014; Schickhoff et al. 2015, 2016; Chhetri and Cairns 2015).

16.5 Conclusion

Changes in tree dbh, and tree and recruit height and density are species-specific and occur with varying degree of abruptness along the treeline ecotone. We identified several tree species lines inside the ecotone. The stand structure is complex; high standard deviations from mean values indicate heterogeneous patterns, differing between different slopes, species and altitudinal zones. Soil temperatures rather than lapse rate air temperatures are associated with physiognomic transitions, treeline position, and spatial regeneration patterns. Thus, the Rolwaling treeline is potentially susceptible to climate change and treeline tree species have the potential to migrate upslope in future with *S. microphylla* showing particularly high dynamics. Upslope migration, however, is effectively controlled by the dense krummholz belt. Currently, the treeline is rather stable; however we found a prolific regeneration as well as signs of stand densification. Further investigations including dendroecological analyses will clarify the complex conditions for establishment and development from recruits to trees. Moreover, investigations at additional Rolwaling study sites and in other valleys are needed to better understand the spatial heterogeneity of Himalayan treeline ecotones and their responsiveness to climate change.

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Scientific publications and conference contributions

Scientific papers (peer-reviewed)

- Müller M, Schickhoff U, Drollinger S, Böhner J, Chaudhary RP, Scholten T (2016) How do soil properties affect alpine treelines? General principles in a global perspective and novel findings from Rolwaling Himal, Nepal. *Progress in Physical Geography* 40(1): 135-160, doi: 10.1177/0309133315615802.

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Other publications (book chapters, peer-reviewed)

- Gerlitz L, Bechtel B, Böhner J, Bobrowski M, Bürzle B, Müller M, Scholten T, Schickhoff U, Schwab N, Weidinger J (2016) Analytic comparison of temperature lapse rates and precipitation gradients in a Himalayan treeline environment – Implications for statistical downscaling. In: Singh ED, Schickhoff U, Mal S (Eds.) *Climate Change, Glacier Response, and Vegetation Dynamics in the Himalaya: Contributions towards Future Earth Initiatives.* Springer, pp. 49-64.

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Conference contributions

- Müller M and Scholten T (2013) Bodenkundliche Steuergrößen der Lage des Waldgrenzökotons im Rolwaling Himal, Nepal, in Reaktion auf den Klimawandel. Jahrestagung der DBG 2013, Rostock. *[talk]*
- Müller M, Drollinger S, and Scholten T (2014) Soil properties and nutrient cycling in the alpine treeline ecotone of Rolwaling Himal, Nepal. IGU (International Geographical Union) Regional Conference 2014, Cracow/Poland. *[talk and poster]*
- Müller M and Scholten T (2014) Soil properties and nutrient cycling in an alpine treeline ecotone of Rolwaling Himal, Nepal. ELS (The Earth Living Skin: Soil, Life and Climate Changes. EGU – SSS Conference), Bari/Italy *[talk]*
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- Drollinger S, Müller M, and Scholten T (2015) Nutrient limitation in soils and trees of a treeline ecotone in Rolwaling Himal, Nepal. EGU 2015. Wien *[talk and poster]*
- Müller M and Scholten T (2015): Der Einfluss von Bodeneigenschaften auf ein Waldgrenzökoton im Rolwaling Himal, Nepal. Jahrestagung der DBG 2015. München *[talk]*