Journal of Biogeography (*J. Biogeogr.*) (2017)

Journal of Biogeography

ORIGINAL ARTICLE

Does tree growth sensitivity to warming trends vary according to treeline form?

Václav Treml[1]* and Thomas T. Veblen[2]

[1]Department of Physical Geography and Geoecology, Faculty of Science, Charles University in Prague, Albertov 6, CZ12843 Prague, Czech Republic, [2]Department of Geography, University of Colorado, Boulder, CO 80309-0260, USA

ABSTRACT

Aim Whereas many treelines are advancing coincident with climate warming, many other treelines are stationary. Differential sensitivity to warming trends may be partially accounted for by differences in the climatic limits associated with distinct treeline forms such as diffuse, abrupt and krummholz treelines. We tested the hypothesis that only diffuse treelines are strictly growth-limited by low temperatures and thus should benefit from warming more than abrupt or krummholz treelines.

Location Colorado Front Range, USA

Methods The growth-climate responses of trees growing at different treeline forms were examined. We built tree-ring chronologies from seven sites covering diffuse, abrupt and krummholz treelines for two conifer species – *Abies lasiocarpa* and *Picea engelmannii*. These chronologies were correlated with climatic variables and compared in terms of growth trends.

Results The variance in tree-ring width chronologies was primarily attributed to tree species and secondarily to treeline form. Tree growth at krummholz sites was limited by the length of the growing season, and ring widths of trees at abrupt treelines also showed a strong drought signal. The growth-climate response of diffuse treelines varied by sites and trees, showing mostly a mixed climatic signal. In general, trees limited by the length of the growing season or by the growing season temperatures were characterized by the increasing growth rates during the last three decades, whereas trees limited by other factors displayed ambiguous growth trends.

Main conclusions Recent growth increase was most pronounced for *Picea engelmannii* at the krummholz treeline form. As a refinement of the treeline form framework, we suggest that temperature-limited tree growth at krummholz treelines may be important, whereas the main common feature of diffuse treelines is their population dynamics and not temperature-limited radial growth. Our results highlight the importance of considering differences in species and treeline form in projecting future treeline advances under a warming climate.

*Correspondence: Václav Treml, Department of Physical Geography and Geoecology, Faculty of Science, Charles University in Prague, Albertov 6, CZ12843 Prague, Czech Republic.
E-mail: treml@natur.cuni.cz

Keywords

***Abies lasiocarpa*, alpine treeline, climate change, dendroecology, krummholz, *Picea engelmannii*, Rocky Mountains, vegetation shift**

INTRODUCTION

Alpine treeline is the temperature-limited upper elevation boundary of the tree life form (Körner, 2012). As such, treeline is defined as a potential line, where tree growth is limited by short growing season and/or low growing season temperatures; above the treeline, wood production is not sufficient to sustain the tree life form (Körner, 2012). Many

doi:10.1111/jbi.12996

upper tree limits, however, are situated at elevations lower than the potential temperature-limited treeline because of other constraints limiting tree occurrence (Holtmeier & Broll, 2005). These constraints include biomass-loss because of snow or wind damage (Kullman, 2005) and insufficient soil moisture or other soil resources for tree seedling establishment and survival (Germino *et al.*, 2002; Macias-Fauria & Johnson, 2013). It has been suggested that the spatial distribution of trees of different sizes and shapes, hereafter referred to as treeline 'forms', reflects the main limiting mechanisms which determines the actual elevation of treelines (Harsch & Bader, 2011). Amongst the four commonly recognized treeline forms (i.e. diffuse, abrupt, island or krummholz) it has been suggested that the temperature control of tree growth is the dominant control mechanism only for the diffuse treeline form (Harsch & Bader, 2011). In contrast, at abrupt, island and krummholz treelines, establishment constraints and biomass-loss, respectively, are considered the primary mechanism restricting tree occurrence (Wiegand *et al.*, 2006; Harsch & Bader, 2011). However, to the best of our knowledge, this conceptual framework linking treeline form to the primary limiting mechanisms of treeline (hereafter treeline form hypothesis) has not been rigorously tested.

Treeline position results from the interplay between tree growth and population dynamics (Holtmeier & Broll, 2005). To explain restricted tree growth at low temperatures, two hypotheses have been recently suggested. The carbon-sink limitation hypothesis, also known as the growth limitation hypothesis, explains low growth through low-temperature limitation on tissue formation (Körner, 2012). In this view, trees are able to assimilate sufficient carbon through photosynthesis but cold temperatures limit the capacity of trees to utilize the carbon for growth. A competing hypothesis is the source limitation hypothesis, which argues that the growth of treeline trees is restricted by the insufficient photosynthesis reflecting low availability of resources (Susiluoto *et al.*, 2010; Sullivan *et al.*, 2015). The prevailing hypothesis is the carbon-sink limitation hypothesis (Simard *et al.*, 2013), which is supported by the global correlation between temperature and treeline position (Körner & Paulsen, 2004) and by the observation that tissue non-structural carbohydrate concentration generally does not decline with greater proximity to treeline (Hoch & Körner, 2012). In comparison with the growth, seedling establishment and survival is more contingent on local conditions including facilitative effects of neighbouring trees (Smith *et al.*, 2003), availability of germination microsites (Dufour-Tremblay *et al.*, 2012), or patterns of snow distribution (Moir *et al.*, 1999).

Assuming broad applicability of the low temperature-induced carbon-sink limitation on the formation of new biomass, recent increases in temperature should be associated with widespread and nearly uniform increases in tree growth and seedling survival. However, a recent synthesis found that only 52% of the global treelines examined exhibited advance whereas 1% retreated and the remainder showed no evidence of change (Harsch *et al.*, 2009). Subsequent studies (e.g., Macias-Fauria & Johnson, 2013; Müller *et al.*, 2016) have further documented the lack of uniform treeline advance, which suggests the significance of factors other than the direct effects of rising temperatures as controls on treeline position. To explain the considerable proportion of treelines not advancing in response to warming, several hypotheses have been offered. First, at least at some treelines, tree establishment is an episodic process with establishment pulses separated by several decades without establishment so that treeline position lags behind the temperature trend (Körner, 2012). A second hypothesis derives from the observation that in many regions trends towards warmer temperatures are also associated with declining moisture availability and reduced snow cover resulting in negative effects on tree seedling survival (Moyes *et al.*, 2015) as well as reduced growth of mature trees in the treeline zone (González de Andrés *et al.*, 2015; Piper *et al.*, 2016). A third hypothesis is based on the recognition of different primary mechanisms controlling the position of treelines according to treeline form. Harsch & Bader (2011) suggested that only diffuse treelines are in equilibrium with growing season temperature and therefore are more likely to be sensitive to warming than other treeline forms. They argue that increases in the growing season temperatures should increase tree growth rates and seedling survival more in diffuse treelines than in other treeline forms. In fact, amongst the 86 treelines examined in Harsch *et al.* (2009), over 80% of the diffuse treelines are advancing in comparison with 22% of the other treeline forms.

In this study, we address the climate influences on tree growth according to treeline forms defined by Harsch & Bader (2011). We recognize that the tree growth and seedling survival may respond differently to warming in the treeline environment (e.g. Camarero & Guitiérrez, 2004; Daniels & Veblen, 2004) and that our study tests only the tree growth but not the population change component of the Harsch & Bader (2011) hypothesis. This study was conducted in the Colorado Front Range, USA, where different treeline forms exist under the same macroclimate with similar regional climatic trends. However, mesoclimatic variability caused by different slope exposures to western winds is reflected in the presence of three different treeline forms – diffuse, abrupt and krummholz. We hypothesize that trees at diffuse treelines should display a stronger positive growth response to growing season temperature than trees at the other two treeline forms. Trees at abrupt treelines are expected to be influenced by factors affecting high seedling mortality, particularly summer droughts (likely well-expressed in tree rings of mature trees), whereas krummholz treelines are governed by winter conditions (less likely expressed in the tree rings of mature trees). To test these hypotheses, we built tree-ring chronologies for each treeline form and two tree species for the analysis of their growth-climate relations and growth trends.

MATERIALS AND METHODS

Geographical setting

The study area is located at elevations of c. 3400 to 3600 m in the forest-alpine ecotone of the Colorado Front Range which is a north-south trending fault block range in northern Colorado (Fig. 1). The subalpine and alpine climates of the Front Range at c. 3000 to 4000 m are highly continental with cold, snowy winters and relatively warm summers. Most precipitation falls in winter and spring with a secondary peak in July and August associated with convective thunderstorms. Despite late summer thunderstorms, summers are relatively dry and availability of moisture restricts tree growth in the subalpine forests (Villalba *et al.*, 1994; Hu *et al.*, 2010). In the subalpine zone at an elevation of 3048 m average annual precipitation is approximately 700 mm, most of which occurs as snow. Mean average annual temperature is around 1.7 °C (C-1 climate data, 1953–2012; Smith *et al.*, 2015). The plant growing season typically runs from May through September as defined by initiation of snowmelt in May and the first series of three consecutive days of frost on average in September (Kittel *et al.*, 2015).

The high elevations of the Front Range encompass a complex elevation gradient from subalpine forest typically dominated by Engelmann spruce [*Picea engelmannii* (Parry) Engelm.] (PIEN hereafter) and subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] (ABLA hereafter) to treeline formed by the same species at c. 3400 m to alpine and unvegetated subnival zones (typically over 3700 m). Instrumental climate records are available since 1953 from Niwot Ridge from a station in the subalpine zone (C1 at 3048 m) and the alpine zone (D1 at 3749 m). Mean annual temperature in the subalpine zone has been warming at a rate of 0.20 °C/decade over the period 1953 to 2008 (McGuire *et al.*, 2012). Although the mean annual temperature in the alpine zone does not show a trend over the 1953 to 2008 period, it shows a non-significant warming trend of 0.41 °C/decade over the 20-year period 1989–2008 (McGuire *et al.*, 2012). Over the 56-year record there has been a tendency towards higher monthly maxima temperatures in July and August which is notably stronger in 1989–2008 (McGuire *et al.*, 2012). Short-term periods (running 5-day averages) of high summer temperatures (> 24 °C) in the subalpine zone have increased markedly since c. 1990 compared with the 1953–1990 period (Smith *et al.*, 2015).

The Niwot Ridge climate stations show contrasting trends in the mean annual precipitation over the period from 1952 to 2010. The alpine station recorded an increase in the mean annual precipitation of 60 mm per decade whereas the subalpine station recorded a non-significant decline of 11 mm per decade (Kittel *et al.*, 2015). The trend towards increasing annual precipitation in the alpine zone was driven primarily by an increase in winter precipitation. At the subalpine site, there was a decrease in the warm season (May-September) precipitation in combination with the increased growing seasonal temperatures and earlier snowpack melt (Kittel *et al.*, 2015). Snowpack (measured as soil water equivalent on April 1) in the subalpine forest has declined by 6% per decade at C1 which is consistent with the regional pattern for subalpine forests in the Front Range (Clow, 2010).

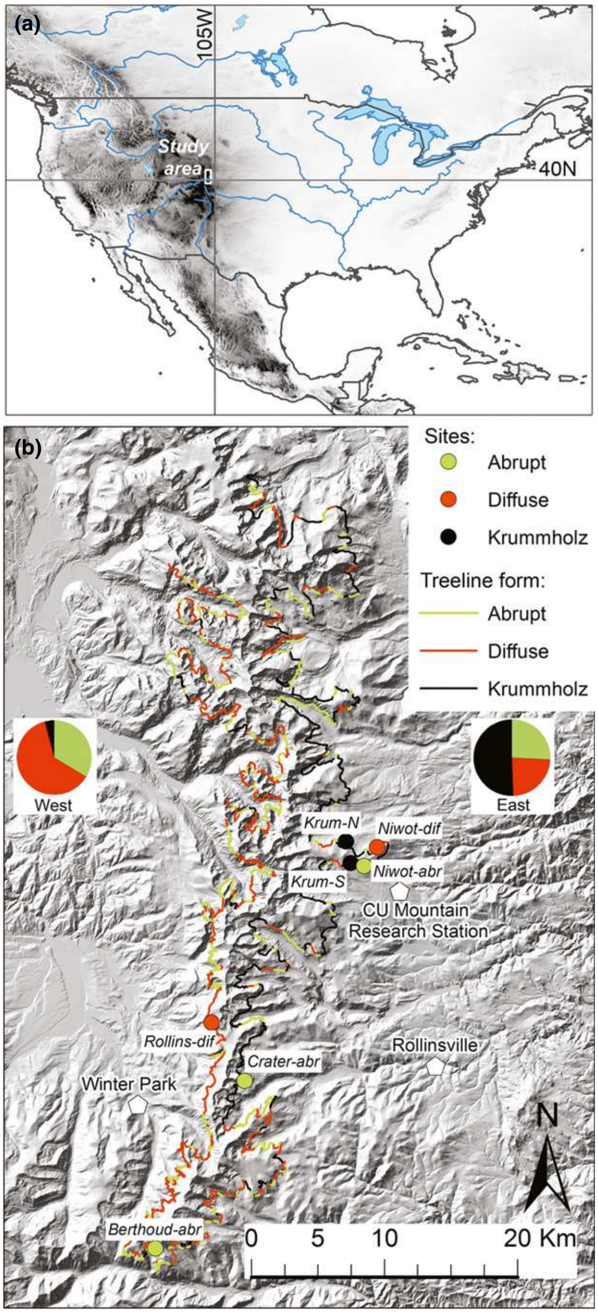

Figure 1 (a) Location of the study area; (b) treeline forms (lines) and locations of sites (filled circles) sampled for tree-growth response to climate variation in the Colorado Front Range. Pie charts in insets refer to percentage lengths of treeline forms west and east from the Continental Divide. Site abbreviations: Krum-S, Niwot krum-S; Krum-N, Niwot krum-N; Niwot-abr, Niwot-abrupt; Niwot-dif, Niwot diffuse; Rollins-dif, Rollins pass; Crater-abr, Crater lake; Berthoud-abr, Berthoud Pass.

Representation of individual treeline forms

Seven sites covering the main treeline forms in the Front Range were selected for tree-ring sampling (Table 1, Fig. 1b). Six sites were located east of the Continental Divide, and one (Rollins Pass) was located to the west. Each treeline form was represented by two sites containing both species; a third site of the abrupt treeline form contained only PIEN.

To evaluate how representative our selected field sites are of treeline forms in the study area, treeline forms were mapped across the Front Range. We performed an on-screen visual classification of orthogonal aerial images with 0.5 m pixel resolution provided by USGS [http://viewer.nationalmap.gov]. At a 1:1000 scale, we classified treeline forms as abrupt, diffuse or krummholz, and determined the lengths of individual treeline forms using the map calculator implemented in ArcInfo 10.3 (ESRI, 2014). Diffuse treelines were recognized by a gradual opening of the forest canopy into individual trees or small tree groups with visible shadows. Abrupt treelines were characterized by the abrupt ending stands with clearly distinguishable individual tree crowns. At abrupt stand margins, shadows of individual trees were frequently observed. Krummholz treelines were characterized by their compact stands lacking distinct tree crown patterns. Stands often consisted of extensive islands, and stand margins did not cast shadows. Classification results were cross-validated by field observations. The proportion of each treeline form was computed for the western and eastern slope of the Continental divide.

Field sampling and sample processing

At each site, 40 individuals each of ABLA and PIEN were cored (Table 1). One core per tree was taken in most cases. Two cores were taken from trees with obviously elliptical stem diameters and the final tree-ring width (TRW) series was derived from the averaged TRWs of both cores. Dominant and co-dominant trees were sampled randomly along two transects across each treeline ecotone. Random selection was supplemented by intentional selection of old trees – ca 10 for each site/species.

At abrupt and diffuse treelines, only trees with upright stems were sampled. At krummholz treelines, sampled PIEN were either specimens with upright basal parts of stems and table-like dense compact canopies at a height of ~2–3 m in the lower part of the ecotone or by vertical stems which had escaped above mats formed by the basal branches and low-stature ramets. Trees sampled in ABLA krummholz stands were the central (and tallest) specimens in compact stands with mat-like margins where the middle part of the stand was formed by upright (often dwarfed) stems in the lower part of ecotone; and in the upper part of the ecotone, sampled stems had escaped above krummholz mats.

Cores were taken at 0.5–1 m stem height. For each tree, stem girth at 0.5 m was measured and tree height was estimated. Tree-ring cores were attached to wooden mounts, air-dried and sanded (Speer, 2010). Ring widths on 620 tree-ring cores were measured using the WinDendro Regular image analysis system (Regent Instruments, 2012).

Growth-climate responses

Tree-ring series were visually cross-dated with the help of statistical indices (*t*-test, dating index, *Gleichläufigkeit*; Speer, 2010). To remove age trends in tree growth, individual TRW series were standardized using 90-year splines (approximately corresponding to mean segment length) and signal-free detrending was applied (Melvin & Briffa, 2008). TRW indices were calculated as ratios (observed/expected TRW), autocorrelation was removed, and final residual chronologies were built using a bi-weight robust mean (Fritts, 2001). Tree cores from trees younger than ca 40 years were not included, however, each chronology still contained more than 30 trees. To suppress the possible effects of high growth variation in the

Table 1 Treeline site and ring-width chronology characteristics of *Picea engelmannii* and *Abies lasiocarpa*.

Site	Elevation (m asl)	Aspect	Slope (°)	Treeline form	Species	Tree height PIEN ABLA (m ± SD)	Chronology start (PIEN, ABLA)	EPS > 0.85 PIEN ABLA	Mean sensitivity PIEN ABLA	Mean/median tree age PIEN ABLA
Niwot Krum-S	3410	S	12	Krummholz	PIEN,ABLA	5.1 ± 0.1	1681,1807	1900	0.229	80/74
						5.2 ± 0.1		1915	0.211	84/81
Niwot Krum-N	3420	N	6	Krummholz	PIEN,ABLA	5.3 ± 0.1	1722,1828	1880	0.231	80/72
						5.3 ± 0.1		1920	0.196	82/80
Niwot-diffuse	3405	NW	17	Diffuse	PIEN,ABLA	6.6 ± 0.1	1860,1881	1915	0.181	76/72
						6.8 ± 0.2		1925	0.211	80/78
Rollins Pass	3520	W	16	Diffuse	PIEN,ABLA	5.5 ± 0.1	1892,1886	1930	0.213	76/72
						5.3 ± 0.1		1925	0.241	83/79
Niwot-abrupt	3410	SW	15	Abrupt	PIEN	6.9 ± 0.2	1862	1900	0.187	76/71
Crater lake	3420	S	15	Abrupt	PIEN,ABLA	7.7 ± 0.6	1893,1868	1930	0.223	75/71
						7.1 ± 0.2		1930	0.220	88/84
Berthoud Pass	3580	SW	26	Abrupt	PIEN,ABLA	7.9 ± 0.5	1863,1870	1900	0.200	82/78
						7.0 ± 0.2		1925	0.197	87/85

Note that tree ages in the last column apply for subsamples used for the trend analyses.

early life stages, growth-climate relations were analysed over the period 1950–2014, i.e. in the period with sufficient representation of mature individuals in all chronologies.

Climatic data were represented by mean, maximum and minimum monthly temperatures and by monthly precipitation from the PRISM database (Daly *et al.*, 2004). We calculated bootstrapped correlations and response functions over a dendrochronological year from May of the year preceding tree-ring formation to September of the ring-formation year (Biondi & Waikul, 2004). Variance in TRW explained by climatic variables was calculated. To cope with multicollinearity and a high number of variables, principal components for temperature and precipitation were computed and entered into the linear model of climate and radial growth. The best model was selected based on the Akaike information criterion. Hierarchical partitioning (Walsh & MacNally, 2004; R package 'hier.part') was applied to estimate the proportion of variance explained by individual variables. The significance of individual variables in hierarchical partitioning was tested by a Monte Carlo permutation test with 100 iterations. Correlations between variance explained by climate and growth rates (indicated by mean TRW) were computed. Principal component analysis, computation of linear model and hierarchical partitioning were performed using R 3.1 (R Development Core Team, 2014).

Growth trends

To compare the growth trends amongst sites and species, individual site/species datasets should be similar in terms of proportions of old and juvenile individuals and mean/median ages. Therefore, subsamples of ~ 30 trees per each site were selected to equalize age representation (Table 1). After detrending using 90 year splines, standard signal-free chronologies were built (Melvin & Briffa, 2008). To emphasize multidecadal growth variability, chronologies were filtered by 20-year low-pass Gaussian filters. To discern possible relations between the strength of temperature response of chronologies and recent growth trends (1990–2014), we calculated Spearman rank correlations between maximum growth responses (i.e. the highest correlation coefficients of TRW chronologies and monthly temperatures) and the slopes of the linear fits of chronologies. Slopes of linear fits were computed for the 1990 to 2014 period of pronounced temperature increase (McGuire *et al.*, 2012). The same analysis was done for precipitation. To determine if there is coherence between climate and tree growth on decadal time scale, TRW chronologies and climate variables were transformed to have zero means and unit variance and then smoothed by a 20-year low-pass Gaussian filter. Growth trends were then compared between key climatic variables and TRW chronologies.

Differences amongst chronologies

Redundancy analysis (RDA; Šmilauer & Lepš, 2014) was applied to estimate the effect of treeline form, tree species and site location on similarity of tree growth patterns, both for standard and residual chronologies. Furthermore, differences in growth rates indicated by the mean ring widths amongst treeline forms were tested using ANOVA on subsamples of similar aged trees. Cohorts of trees established in 1930s and 1940s, well represented at all sites, were selected for this purpose.

RESULTS

We compiled 13 tree-ring width chronologies including 520 trees and covering six sites for ABLA and seven sites for PIEN (Table 1). Our sampled sites are representative of the treeline forms in the Colorado Front Range which include diffuse (40%), krummholz (31%) and abrupt treelines (29%) (Fig. 1). West of the Continental Divide, the most extensive treeline form was the diffuse form whereas in east of the Divide, the krummholz form was predominated (Fig. 1, Appendix S1). The oldest trees were PIEN from krummholz sites with several individuals established in 17th and 18th centuries. PIEN chronologies from abrupt and diffuse treelines extended back to the late 19th century (Table 1). The oldest ABLA samples dated to 1860–70s uniformly for almost all sites.

Mean TRWs of PIEN were well-differentiated by treeline form. PIEN at diffuse treelines exhibited the highest growth rates, whereas PIEN trees from krummholz treelines had the lowest growth rates ($P < 0.05$; Fig. 2). Growth rates of PIEN at abrupt treelines were intermediate between krummholz and diffuse treelines. ABLA growth rates showed no significant differences amongst treeline forms (Fig. 2). For each treeline form and species, between-site differences in mean TRW were not significant ($P > 0.05$, Tukey post-hoc test). The only exception was ABLA at diffuse treeline with significantly higher growth rates at the Niwot-diffuse site in

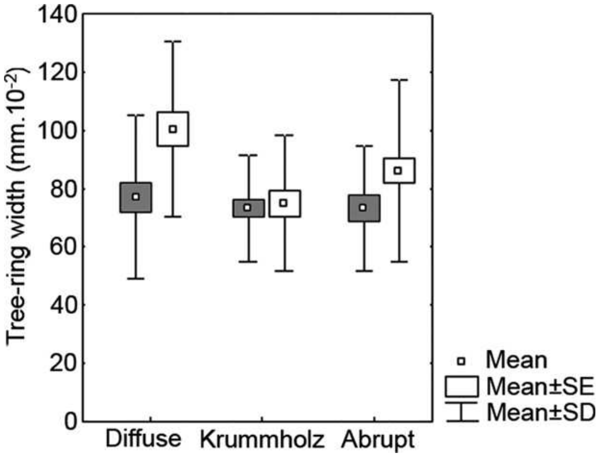

Figure 2 Comparison of radial growth rates of same-aged trees (cohorts established in 1930s and 1940s) among the three treeline forms. Empty boxes denote *Picea engelmannii*, grey boxes denote *Abies lasiocarpa*. Abbreviations: SE, standard error, SD, standard deviation.

comparison to the Rollins Pass site ($P < 0.05$, Tukey post-hoc test).

Variance in the tree-ring chronologies was attributed particularly to tree species (Fig. 3). The first axis of the RDA explained 18% of the variance, and correlations of ABLA and PIEN with Axis 1 were 0.82 and −0.84, respectively (Fig. 3). Additional variance was explained by Axis 2 (16%) which was particularly correlated with the krummholz treeline form. A relatively low portion of variance (5%) captured differences between the abrupt and diffuse treelines along axis 4 (not shown).

Standard TRW chronologies at all treeline forms and for both species show two common decadal-scale patterns (Fig. 4a). First, radial growth was above the average in the 1940s. Second, a pronounced growth depression occurred in 1970s and 1980s. Growth trends of krummholz PIEN sites display strong growth increases since the 1990s. PIEN at abrupt treelines increased its growth less than at the krummholz treelines. The growth of PIEN at diffuse treelines since the early 1990s was site-dependent – the Rollins Pass site, located west of the Continental Divide, showed a pronounced growth increase whereas the diffuse treeline form at the Niwot site did not show any trend. The recent growth increase of ABLA chronologies was generally much less than that of PIEN across all the treeline forms. There were no consistent differences in the recent growth trends amongst treeline forms for ABLA. Variability in decadal trends of TRW chronologies for both species and all the three treeline forms were highest during the last 10 years (2005–2014) (Fig. 4b).

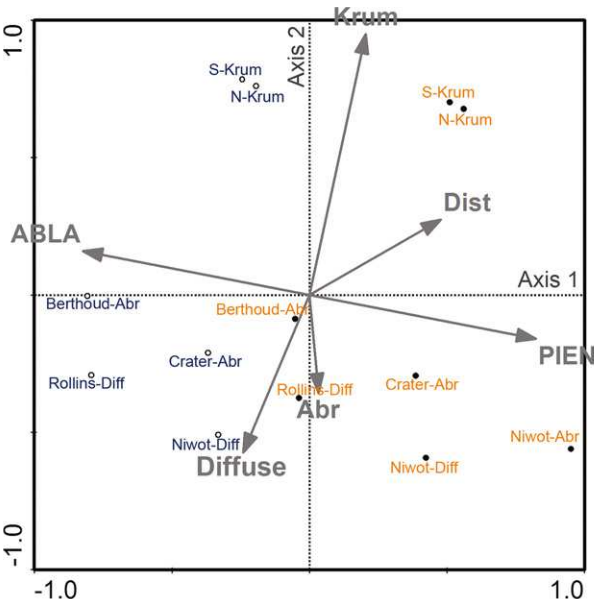

Figure 3 Ordination plot (redundancy analysis) of TRW chronologies (response variables) and tree species, treeline form and site position (explanatory variables). The length of the arrows is proportional to correlation with a given axis. *Abies lasiocarpa* sites are indicated in blue, *Picea engelmannii* in orange. Abbreviations: Krum, krummholz; Abr, abrupt; Dist, distance from northernmost site.

Growth-climate relationships common to both species and all treeline forms include a positive relationship of TRW to preceding October temperatures (mean, maximum and minimum), to maximum May temperature of the current growing season, and to preceding July precipitation (Fig. 5). Krummholz treelines showed the strongest response to May temperature of the current growing season amongst all treeline forms. Correlation coefficients between May mean temperature and TRW of PIEN chronologies were 0.51 and 0.46 for south and north-facing Niwot krummholz sites, respectively. Furthermore, the krummholz treeline sites showed consistent negative responses to precipitaion in April and May. Radial growth at abrupt treelines displayed relatively higher correlation coefficients with preceding July precipitation than the other treeline forms (0.38, 0.44, and 0.36 for ABLA Crater lake, ABLA Berthoud Pass and PIEN Niwot-abrupt, respectively). Tendencies towards negative correlations of tree growth with maximum temperatures of the preceding July and August were strongest for the abrupt treeline form and especially so for ABLA. Compared with PIEN across all treeline forms, ABLA was more limited by precipitation and maximum temperature in the year preceding tree-ring formation (i.e., positive correlation with July precipitation, and negative correlation with July maximum temperature) as well as precipitation in June of the year of ring formation (i.e. positive correlation). Growth-climate responses of trees at diffuse treelines differed amongst sites (Fig. 5). Whilst Rollins Pass PIEN and ABLA showed a strong climate signal driven mainly by temperature, the climatic signal in the chronologies from the Niwot-diffuse site was weaker and driven mainly by precipitation (Fig. 5).

The amount of variance explained by climatic variables was highest for krummholz treelines, with the dominant effect being temperature PCs for PIEN and both temperature and precipitation PCs for ABLA (Fig. 6). At abrupt treelines, a major part of the variance was explained by precipitation PCs both for PIEN and ABLA with the exception of the Berthoud Pass PIEN chronology. For diffuse treelines, a prevailing influence of precipitation PCs (Niwot-diffuse site), or importance of both precipitation and temperature PCs was observed.

Comparison of tree growth and decadal-scale climatic variation showed that the PIEN chronologies are coherent particularly with temperature in May (both krummholz sites, Niwot-abrupt, Crater-abrupt, Niwot-diffuse; Appendix S2). This is less apparent for ABLA, although there is coherency between TRW and precipitation in July and/or preceding temperature in October for some sites (Niwot Krum-N, Berthoud Pass, Rollins Pass, Niwot-diffuse). The recent growth increase of the PIEN at abrupt treelines follows an increase in July precipitation.

To explain the high variability of slopes of TRW chronologies between 1990 and 2014, we correlated the slope of the

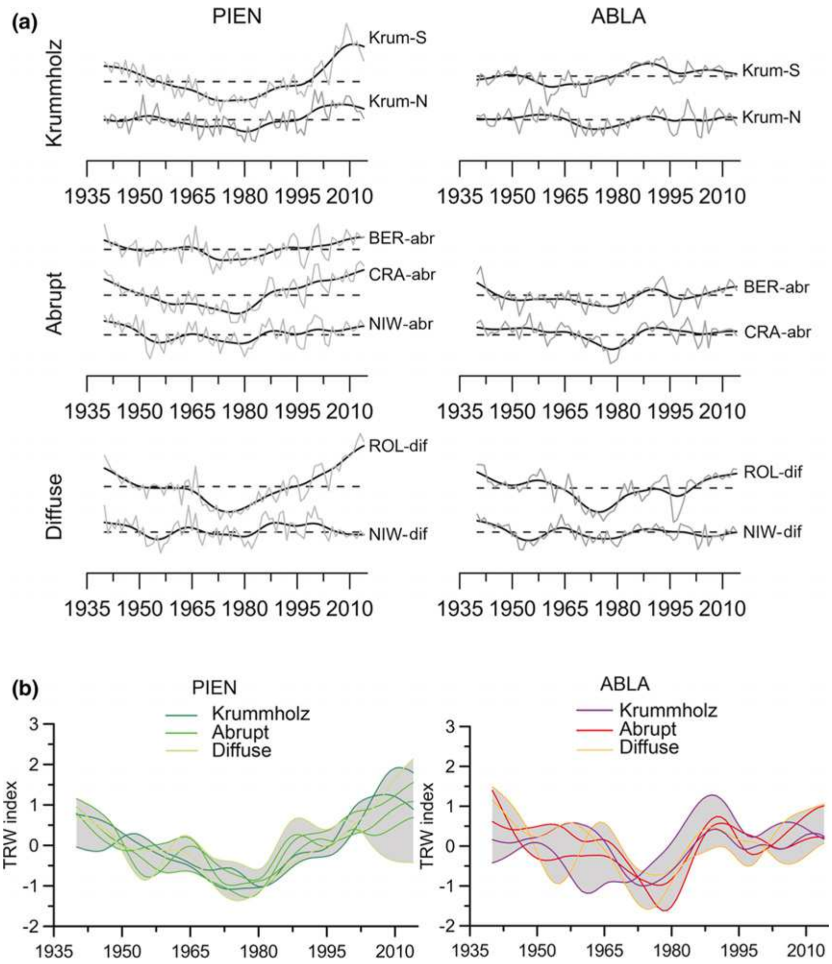

Figure 4 (a) Standard tree-ring chronologies and growth trends as indicated by 20 year low-pass filters. Dashed line indicates TRW index = 1. Abbreviations for sites: Krum-S, krummholz-south; Krum-N, krummholz-north; BER, Berthoud; CRA, Crater Lake; ROL, Rollins Pass; NIW-A, Niwot-Abrupt; NIW-D, Niwot-Diffuse. (b) Plots of growth trends for all thirteen TRW chronologies. TRW chronologies were smoothed by 20 year low-pass filters.

linear growth trend (i.e. regression coefficient) with the strongest climate response for each site chronology as represented by the correlation coefficient between TRW and temperature or precipitation. There is a significant correlation (Spearman $r = 0.69$, $P < 0.01$) between the slopes of recent growth trends (1990–2014) and maximum temperature responses of chronologies (Appendix S3). The relationship of the trend slopes with the precipitation correlation coefficients was negative (Appendix S3), but not statistically significant (Spearman $r = -0.45$, $P = 0.11$).

DISCUSSION

As predicted by the treeline form framework (Harsch & Bader, 2011), we expected that the growth-climate responses of trees growing at diffuse, abrupt and krummholz treelines would differ and, hence, their climatic limitations would not be identical. Indeed, we observed distinct treeline form-specific growth-climate responses, but also responses that were common amongst treeline forms. The latter involves a positive response of radial growth to temperature in the October preceding the ring-formation season, to May temperature of the current growing season, and to precipitation in the preceding July.

In contrast to our expectation that only the diffuse treeline would show a favourable response to warming of growing season temperatures, the growth-climate response of diffuse treelines was highly variable and not stronger than the response at krummholz sites. Whilst the Rollins Pass site showed a rather strong temperature response to the preceding fall and to the first half of the growing season, the Niwot-diffuse treeline site exhibited a weak mixed climatic signal. Both diffuse treeline sites were similar in their age structures (with a substantial proportion of young trees) and in high growth rates of PIEN, but differed in climate signals. The major common attribute of diffuse treelines was the unconstrained seedling establishment, survival and growth to tree size, which, in some cases (Rollins Pass) allowed tree stands to approach their temperature limit. Considering radial growth, we did not find much support for growth limiting conditions at diffuse treelines because tree rings were as wide or wider (PIEN) than at other treeline forms (ABLA). However, we did not measure the height growth, which could be more sensitive to limiting conditions compared with radial increment (Paulsen *et al.*, 2000).

At krummholz treelines, by far the strongest correlation was with May temperatures in the year of tree-ring formation (i.e. when most of these treeline stands may still be

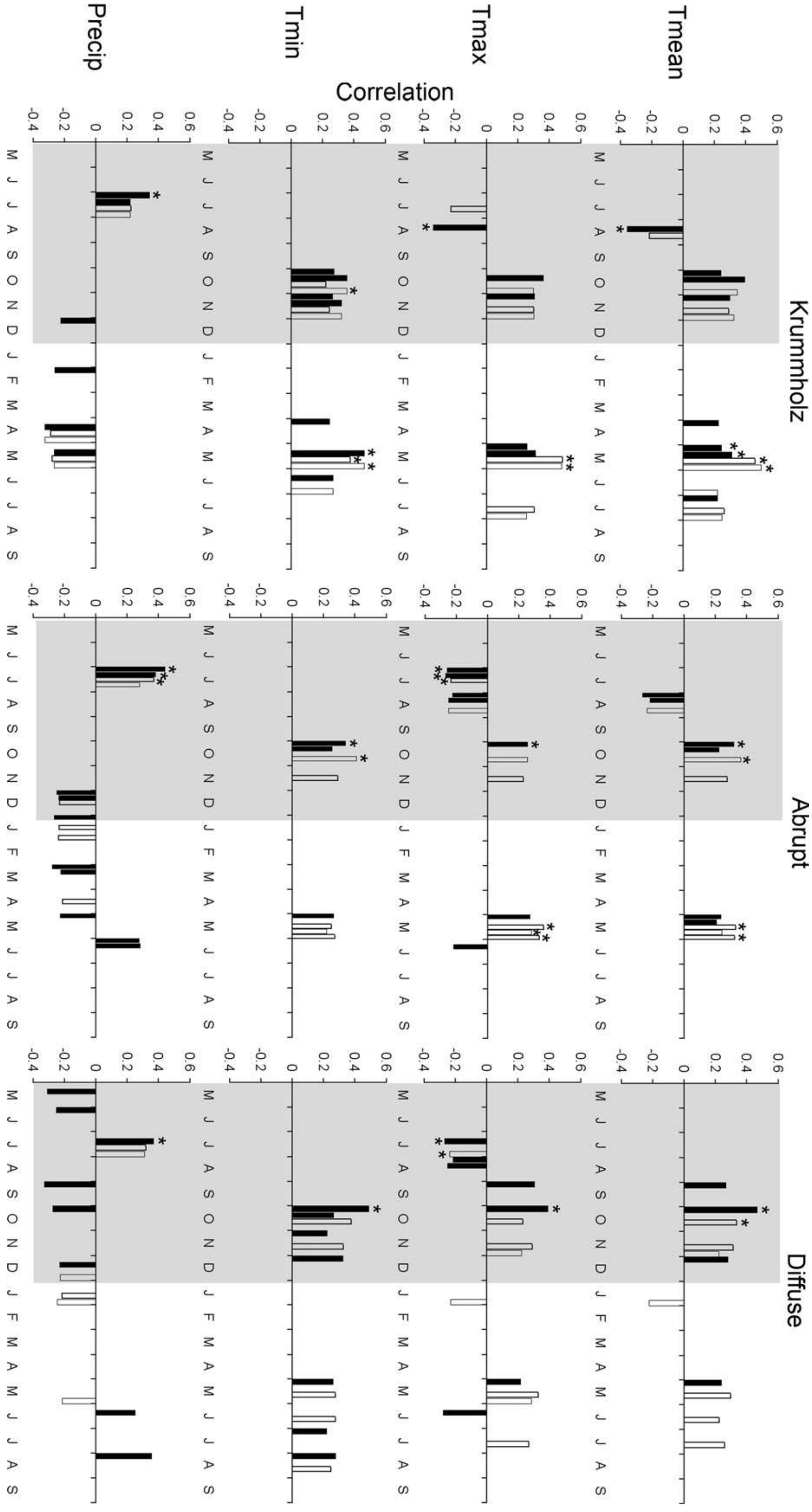

Figure 5 Statistically significant correlations (columns) and responses (asterisks) of TRW and climatic variables (average mean, maximum and minimum monthly temperatures, monthly precipitation sums). Full and empty columns denote *Abies lasiocarpa* and *Picea engelmannii* respectively. Gray part of the graph refers to months of the year preceding to tree-ring formation season.

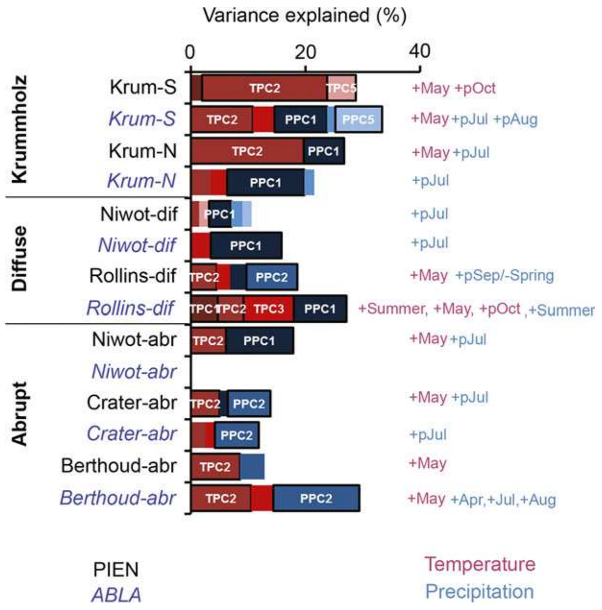

Figure 6 Amount of explained variance in TRW chronologies by climatic variables simplified using principal component analysis. Variance explained by temperature (red) and precipitation (blue) principal components included in the best model was estimated by hierarchical partitioning. The size of each column partition is proportional to the independent effect of a given variable. Statistically significant ($P < 0.05$) independent effects are indicated by a bold black frame. The codes are designed as follows: TPC2 = temperature, principal component axis 2; etc. Temperature and precipitation variables having the highest loadings in significant principal components are indicated next to columns.

covered by snow pack). We suggest that this observed climate signal is indicative of a favourable influence of earlier initiation of the growing season associated with earlier snowmelt because of high May temperatures (Clow, 2010). Negative correlations of growth and spring precipitation (April, May) are consistent with this interpretation; April and May precipitation falls mostly as snow and thus delays snowmelt. Treeline trees in the study area are characterized by a growing season of approximately 100 days inferred from the date of snowmelt and the date of the decline of mean daily temperature below 0.9 °C at the growing season end (following Paulsen & Körner, 2014). However, krummholz sites are mostly situated in snow accumulation areas and their growing season is therefore even shorter than for the average treeline in the study area, with complete snowmelt as late as during July (Cline, 1997; Harpold *et al.*, 2015). Growing season length at krummholz sites thus approaches the lower limit of the growing season duration for conifers which has been estimated in the range from 86 to 90 days (Paulsen & Körner, 2014; Rossi *et al.*, 2016). Snowmelt is a very important driver of the beginning of wood formation (Treml. *et al.*, 2015). It is well-known that the later the wood formation starts the shorter the growing season and the lesser the amount of wood formation (Rossi *et al.*, 2016). An extremely short growing season thus results in low amounts of tree growth and reduced probability that the stem height is sufficient to lift foliage above the ice-blasted layer above the snow surface. Consequently, upright tree stems are not formed in the krummholz treelines. Strong growth inhibition by mechanical damage is important for the formation of krummholz treeline (Cairns, 2005; Wiegand *et al.*, 2006), but according to our results, this inhibition results from the interaction of mechanical damage and very low growth. Enhanced growth at krummholz treelines was not related to either winter warming or to increases in winter precipitation as reported for some sites with advancing krummholz treelines (Lescop-Sinclair & Payette, 1995; Harsch *et al.*, 2009). The substantial radial growth increase recorded in our study reflects the presence of some upright stems protruding above the low krummholz mats.

The TRW chronologies from the abrupt treelines showed that drought stress is an important limitation to tree growth in this treeline form. This finding is in agreement with the hypothesis that abrupt treelines are more likely to be limited by moisture availability. The drought signal observed in tree rings of mature trees in our study is consistent with the findings of high seedling mortality in open grasslands adjacent to treeline attributed to drought or excessive radiation (Weisberg & Baker, 1995; Germino *et al.*, 2002).

Since there were both different and common growth-climate responses amongst the three treeline forms, we considered the climate sensitivity of TRW chronologies at individual sites. The principal common decadal-scale pattern for both species across all seven sites was the growth depression in 1970s and 1980s. This period was characterized by relatively low May temperatures as well as by low July precipitation. Low May temperature coincides with growth depression most consistently for the PIEN chronologies. The patterns for the ABLA chronologies are more complex and include apparent effects of cooler preceding October as well as May temperature and summer precipitation during the 1970s–1980s. After 1990, growth trends varied substantially between the two tree species and amongst treeline forms resulting in the highest variability across the 13 chronologies after 2005. Overall, there was a strong relationship between positive growth trends and rising temperatures after 1990. The most consistent recent increase in growth was for PIEN and its greatest magnitude was for the krummholz treelines. Indeed, there were significant increasing trends in maximum spring and summer temperature in the study area since 1950s (McGuire *et al.*, 2012) as well as earlier snowmelt (Clow, 2010). In addition, recent increases in tree growth (e.g. for PIEN at the abrupt treeline sites and at the Rollins Pass diffuse site) coincide with increases in July precipitation. Species differences as well as site differences in sensitivity to summer precipitation contribute to the high degree of variability in recent growth trends.

Growth-climate analyses in the current study revealed sensitivity of radial growth to temperatures at the beginning of the growing season (e.g. May) which implies a limitation of growing season length on the ability of trees to form xylem cells (Cuny *et al.*, 2014). Furthermore, the growth of treeline trees was positively correlated with the temperature during the growing season which is associated with the temperature-affected rate of xylogenesis (Cuny *et al.*, 2014). We also observed a positive correlation of radial growth with temperature in the fall (October) preceding the ring-formation year. This is usually interpreted as an early-growing season utilization of carbon reserves stored at the end of the preceding season when there is no growth (i.e. no carbon sink; Oberhuber, 2004). Some of the treeline chronologies were negatively correlated with maximum temperatures in the preceding growing season implying either drought-limited resource accumulation or low foliage area on smaller shoots affecting growth during the following season.

In addition to the temperature influences on growth, we identified positive responses to growing seasonal precipitation, which may directly affect the rate of xylogenesis (Deslauriers *et al.*, 2016). The positive correlation with precipitation during the preceding growing season may be the consequence of resource accumulation, foliage surface or plant organ mortality (either individually or in combination) affected by the climate in the year preceeding to tree-ring formation (Oribe *et al.*, 2003; Brunner *et al.*, 2015). The strong effect of the growing season duration as well as availability of resources at the beginning of the growing season may be particularly important in controlling growth of trees in environments with an extremely short growing season, such as at treeline in the Front Range.

In addition to showing that trees growing at different treeline forms respond differently to climate variation, our results also identified consistent differences between PIEN and ABLA. We found a stronger drought signal in the growth of ABLA compared with PIEN. The reduced abundance of ABLA at abrupt treeline sites may also be related to a greater sensitivity to drought. These results are consistent with previous research showing a greater sensitivity of the growth of ABLA compared with PIEN to precipitation limitation in nearby subalpine forests (Villalba *et al.*, 1994). Our results suggest that the tree species has a greater impact on tree growth response to climate variation than do mechanisms underlying variability in treeline form, yet both types of variables affected tree growth response to climate.

Overall, our findings imply that the regional response of treeline to warming temperatures is unlikely to consist of a uniformly rising treeline. Instead, tree growth responses to warming near treeline are contingent on species, treeline form, and site factors affecting moisture availability. The strongest differences in growth patterns were between the krummholz treeline form and the remaining treeline forms - diffuse and abrupt. Growth of krummholz treelines was particularly limited by the length of the growing season. Tree growth at abrupt treelines showed a consistent drought signal whereas growth at diffuse treelines was more site-specific revealing either a growing season temperature signal or a mixed climatic signal including both temperature and precipitation. Treeline chronologies showing positive correlations with temperatures were characterized by increased radial growth since c. 1990 in conjunction with warming temperatures, whereas treeline chronologies with a drought signal revealed a smaller or no increase in growth since the early 1990s. Recent warming has been more beneficial to the growth of PIEN compared to ABLA in the treeline ecotone. These results highlight the importance of considering differences in species and treeline form in projecting future treeline advances under a warming climate.

ACKNOWLEDGEMENTS

Research support was provided by the Fulbright commission to V. Treml and Award No. 1262687 of the U.S. National Science Foundation to T.T. Veblen. For field and logistical assistance we thank R. Andrus, B. Harvey and G. Ornelas. Logistical support and climate data were provided by the Mountain Research Station of the University of Colorado Boulder and the Niwot Ridge Long Term Ecological Research (NWT LTER) of the National Science Foundation. We thank three anonymous reviewers and the associate editor for their helpful comments on an earlier version of the paper.

REFERENCES

Biondi, F. & Waikul, K. (2004) DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computer Geosciences*, **30**, 303–311.

Brunner, I., Herzog, C., Dawes, M.A., Arend, M. & Sperisen, C. (2015) How tree roots respond to drought. *Frontiers in Plant Science*, **6**, 547.

Cairns, D.M. (2005) Simulating carbon balance at treeline for krummholz and dwarf tree growth forms. *Ecological Modelling*, **187**, 314–328.

Camarero, J.J. & Guitiérrez, E. (2004) Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. *Climatic Change*, **63**, 181–200.

Cline, D.W. (1997) Snow surface energy exchanges and snowmelt at a continental, midlatitude Alpine site. *Water Resources Research*, **33**, 689–701.

Clow, D.W. (2010) Changes in the timing of snowmelt and streamflow in Colorado: a response to recent warming. *Journal of Climate*, **23**, 2293–2306.

Cuny, E.H., Rathgeber, C.B.K., Frank, D., Fonti, P. & Fournier, M. (2014) Kinetics of tracheid development explain conifer tree-ring structure. *New Phytologist*, **203**, 1231–1241.

Daly, C., Gibson, W.P., Doggett, M., Smith, J. & Taylor, G. (2004) Up-to-date monthly climate maps for the conterminous United States. 84th AMS Annual Meeting Combined Preprints, Seattle, Paper P5.1.

Daniels, L.D. & Veblen, T.T. (2004) Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. *Ecology*, **85**, 1284–1296.

Deslauriers, A., Huang, J.-G., Balducci, L., Beaulieu, M. & Rossi, S. (2016) The contribution of carbon and water in modulating wood formation in black spruce saplings. *Plant Physiology*, **170**, 2072–2084.

Dufour-Tremblay, G., De Vriendt, L., Lévesque, E. & Boudreau, S. (2012) The importance of ecological constraints on the control of multi-species treeline dynamics in eastern Nunavik, Québec. *American Journal of Botany*, **99**, 1638–1646.

ESRI (2014) *ArcGIS*. Environmental Systems Research Institute, Redlands.

Fritts, H.C. (2001) *Tree rings and climate*. Blackburn press, Caldwell.

Germino, M.J., Smith, W.K. & Resor, A. (2002) Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecology*, **162**, 157–168.

González de Andrés, E., Camarero, J.J. & Büntgen, U. (2015) Complex climate constraints of upper treeline formation in the Pyrenees. *Trees*, **29**, 941–952.

Harpold, A.A., Molotch, N.P., Musselman, K.N., Bales, R.K., Kirchner, P.B., Litvak, M. & Brooks, P.D. (2015) Soil moisture response to snowmelt timing in mixed-conifer subalpine forests. *Hydrological Processes*, **29**, 2782–2798.

Harsch, M.A. & Bader, M.Y. (2011) Treeline form—A potential key to understanding treeline dynamics. *Global Ecology and Biogeography*, **20**, 582–596.

Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R. (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, **12**, 1040–1049.

Hoch, G. & Körner, C. (2012) Global patterns of mobile carbon stores in trees at the high-elevation tree line. *Global Ecology Biogeography*, **21**, 861–871.

Holtmeier, F.K. & Broll, G. (2005) Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*, **14**, 395–410.

Hu, J., Moore, D.J.P., Burns, S.P. & Monson, R.K. (2010) Longer growing season lead to less carbon sequestration in a subalpine forest. *Global Change Biology*, **16**, 771–783.

Kittel, T.G.F., Williams, M.W., Chowanski, K., Hartman, M., Ackerman, T., Losleben, M. & Blanken, P. (2015) Contrasting long-term alpine and subalpine precipitation trends in a mid-latitude North American mountain system, Colorado Front Range, USA. *Plant Ecology & Diversity*, **8**, 607–624.

Körner, C. (2012) *Alpine treelines – Functional ecology of the global high elevation tree limits*. Springer, Dordrecht.

Körner, C. & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, **31**, 713–732.

Kullman, L. (2005) Wind-conditioned 20th century decline of birch treeline vegetation in the Swedish Scandes. *Arctic*, **58**, 286–294.

Lescop-Sinclair, K. & Payette, S. (1995) Advance of the arctic treeline along the eastern coast of Hudson Bay. *Journal of Ecology*, **83**, 929–936.

Macias-Fauria, M. & Johnson, E.A. (2013) Warming-induced upslope advance of subalpine forest is severely limited by geomorphic processes. *Proceedings of National Academy of Sciences USA*, **110**, 8117–8122.

McGuire, C.R., Nufio, C.R., Bowers, M.D. & Guralnick, R.P. (2012) Elevation-dependent temperature trends in the Rocky Mountain Front Range: changes over a 56- and 20-year record. *PlosOne*, **7**, e44370.

Melvin, T.M. & Briffa, K.R. (2008) A “signal-free” approach to dendroclimatic standardisation. *Dendrochronologia*, **26**, 71–86.

Moir, W.H., Rochelle, S.G. & Schoettle, A.W. (1999) Microscale patterns of tree establishment near upper treeline, Snowy Range, Wyoming, U.S.A. *Arctic, Antarctic, and Alpine Research*, **31**, 379–388.

Moyes, A.B., Germino, M.J. & Kueppers, L.M. (2015) Moisture rivals temperature in limiting photosynthesis by trees establishing beyond their cold-edge range limit under ambient and warmed conditions. *New Phytologist*, **207**, 1005–1014.

Müller, M., Schickhoff, U., Scholten, T., Drollinger, S., Böhner, J. & Chaudhary, R.P. (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**, 135–160.

Oberhuber, W. (2004) Influence of climate on radial growth of *Pinus cembra* within the alpine timberline ecotone. *Tree Physiology*, **24**, 294–301.

Oribe, Y., Funada, R. & Kubo, T. (2003) Relationships between cambial activity, cell differentiation and the localization of starch in storage tissues around the cambium in locally heated stems of *Abies sachalinensis* (Schmidt). *Trees*, **17**, 185–192.

Paulsen, J., Weber, U.M. & Körner, C. (2000) Tree growth near treeline: abrupt or gradual reduction with altitude? *Arctic, Antarctic, and Alpine Research*, **32**, 14–20.

Paulsen, J. & Körner, C. (2014) A climate-based model to predict potential treeline position around the globe. *Alpine Botany*, **124**, 1–12.

Piper, F.I., Viñegla, B., Linares, J.C., Camarero, J.J., Cavieres, L.A. & Fajardo, A. (2016) Mediterranean and temperate treelines are controlled by different environmental drivers. *Journal of Ecology*, **104**, 691–702.

R Development Core Team (2014) *R: a language and environment for statistical computing*. R foundation for statistical computing, Vienna, Austria.

Regent Instruments (2012) *WinDendro Image analysis system*. Regent Instruments Inc., Québec.

Rossi, S., Anfodillo, T., Čufar, K. *et al.* (2016) Pattern of xylem phenology in conifers of cold ecosystems at the northern hemisphere. *Global Change Biology*, **22**, 3804–3813.

Simard, S., Giovanelli, A., Treydte, K., Traversi, M.L., King, G.M., Frank, D. & Fonti, P. (2013) Intra-annual dynamics of non-structural carbohydrates in the cambium of mature conifer trees reflects radial growth demands. *Tree Physiology*, **33**, 913–923.

Šmilauer, P. & Lepš, J. (2014) *Multivariate analysis of ecological data using Canoco 5*. CUP, Cambridge.

Smith, W.K., Germino, M.J., Hancock, T.E. & Johnson, D.M. (2003) Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, **23**, 1101–1112.

Smith, J.M., Paritsis, J., Veblen, T.T. & Chapman, T.B. (2015) Permanent forest plots show accelerating tree mortality in subalpine forests of the Colorado Front Range from 1982 to 2013. *Forest Ecology and Management*, **341**, 8–17.

Speer, J.H. (2010) *Fundamentals of tree-ring research*. The University of Arizona Press, Tucson.

Sullivan, P., Ellison, S., McNown, R., Brownlee, A. & Sveinbjornsson, B. (2015) Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. *Ecology*, **96**, 716–727.

Susiluoto, S., Hilasvuori, E. & Berninger, F. (2010) Testing the growth limitation hypothesis for subarctic Scots pine. *Journal of Ecology*, **98**, 1186–1195.

Treml., V., Kašpar, J., Gryc, V. & Kuželová, H. (2015) Differences in intra-annual wood formation in Picea abies across the treeline ecotone, Giant Mountains, Czech Republic. *Trees*, **29**, 515–526.

Villalba, R., Veblen, T. & Ogden, J. (1994) Climatic influences on the growth of subalpine trees in the Colorado Front Range. *Ecology*, **75**, 1450–1462.

Walsh, C. & MacNally, R. (2004) Hier.part Version 0.5–3. R-package. Available at: http://www.r-project.org.

Weisberg, P.J. & Baker, W.L. (1995) Spatial variation in tree regeneration in the forest-tundra ecotone, Rocky Mountain National Park, Colorado. *Canadian Journal of Forest Research*, **25**, 1326–1339.

Wiegand, T., Camarero, J.J., Rüger, N. & Gutiérrez, E. (2006) Abrupt population changes in treeline ecotones along smooth gradients. *Journal of Ecology*, **94**, 880–892.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Length of individual treeline forms.
Appendix S2 TRW chronologies and climate variables.
Appendix S3 Growth-climate responses and TRW trends.

BIOSKETCHES

Václav Treml is an assistant professor at the Charles University in Prague. His research focuses on tree growth in cold environments and treeline dynamics in general. **Thomas T. Veblen** is Professor of Geography at the University of Colorado Boulder. His research interests include impacts of climate change on forest dynamics and disturbance processes.

Author contributions: V.T. and T.T.V. conceived the ideas; V.T. collected and analysed the data; both authors wrote the manuscript.

Editor: Matt McGlone