Growth cessation of lower margin Qinghai spruce corresponds to years with low early-monsoon precipitation

Running head: Stem-growth cessation corresponds to drought

SHOU DONG ZHAO¹, YUAN JIANG¹*, MANYU DONG¹, HUI XU², NEIL PEDERSON³

¹State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing Normal University, 19 Xinjiekouwai Street, Haidian, 100875 Beijing, China
²Department of Biostatistics and Epidemiology, School of Public Health and Health Sciences, University of Massachusetts Amherst, 131 Brittany Manor Dr. APT G, Amherst, MA 01003, USA
³Harvard Forest, Harvard University, 324 N Main Street, Petersham, MA 01366, USA

*Corresponding author:
Yuan Jiang
State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing Normal University, 19 Xinjiekouwai Street, Haidian, 100875 Beijing, China
Tel: +86 10 58806093; Fax: +86 10 58809274
E-Mail: jiangy@bnu.edu.cn

Abstract
The response of tree growth to climate can vary over time and geographical space. This
study aims to evaluate and compare the climatic drivers of Qinghai spruce (*Picea crassifolia* Kom.), a species endemic to northwest China, over an elevational gradient, from its lower distributional margin to its upper distributional margin. We sampled pure Qinghai spruce stands and obtained time-series of growth from 25 trees each in three populations across its distributional range in the Helan Mountains. We found that trees at the lower distributional margin have lower first-order autocorrelation coefficients in annual growth and have experienced an increase in locally-absent rings (stem-growth cessation) since 2001. While all populations have a similar growth response to climate, trees at lower distributional margin are more sensitive to variations in June precipitation and July vapor pressure deficit (VPD) than populations at higher elevations. Early-monsoonal precipitation, June, appears to be the primary diver of stem-growth cessation events in trees at the lower distributional margin. Evidence indicates that July VPD exacerbates the effect of low June rainfall enough to increase stem-growth cessation in the lower distribution population. Our results find that precipitation is a major driver of Qinghai spruce growth, trees at lower distribution limit are more sensitive to precipitation than at higher elevations, and that high VPD exacerbates stress such that it increases the rate of stem-growth cessation. It seems that the increase in severity and frequency of stem-growth cessation could be a signal of an ecological tipping point in the lower population. Increased vapor pressure deficit and warming in the region would likely exacerbate the stress of low early-monsoonal rainfall on Qinghai spruce growth. If this occurs, it could potentially increase the mortality rate of lower distributional margin trees, especially those that are already experiencing events of temporary growth cessation.
Keywords:
Tree-ring analysis, semi-arid Asia, climate change, drought, species range margins, locally-absent rings

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Introduction

Trees are generally considered to be more sensitive to climate at forest boundaries, e.g. range margins, than in forest interiors (Cernusak & English, 2015); but see Cavin and Jump (2016) for a recent exception. At northern range margins, tree growth is often temperature-limited such that warming increases growth (Bhuta et al., 2009, Cook et al., 1998, D’Orangeville et al., 2016, Lloyd et al., 2011, Shi et al., 2010), although there are notable exceptions for broadleaf trees (Hilasvuori & Berninger, 2010, Pederson et al., 2004, Tardif et al., 2006) and for trees in semi-arid areas (Housset et al., 2015, Liang et al., 2008). In contrast to northern range margins, much research at southern range margins finds that trees are often limited by a lack of soil water and exacerbated by high temperatures (Chhin et al., 2004, Dulamsuren et al., 2011, Galván et al., 2014, Hacket-Pain et al., 2016, Martin-Benito & Pederson, 2015, Urli et al., 2015). Some studies have found that warming has sped up ecological processes in some regions such that there have been range shifts at northern range margins (Boisvert-Marsh et al., 2014, Chen et al., 2011), and growth decline and mortality at southern range margins (Kharuk et al., 2013, Lesica & McCune, 2004,
Peñuelas et al., 2008). From these findings, it becomes apparent that accurate assessments of the response to climate of trees and forests at range margins are needed to better anticipate the impact of climatic change.

Qinghai spruce (*Picea crassifolia* Kom.) is an endemic tree species in semi-arid northwest China (Liang et al., 2006). A little more than 5% of the total biomass of Qinghai spruce is found in the Helan Mountains, a total that is second only to Qilian Mountains for Qinghai spruce (Liu, 1992). Embedded within the large-scale transition from steppe to desert vegetation (Jiang et al., 2007), the Helan Mountains represent the northeastern margin of the Qinghai spruce distribution area making these mountains an important location for Qinghai spruce conservation in the face of climatic change. In the Qilian Mountains, Qinghai spruce growth is sensitive to drought and broadly has a similar climate-growth relationship across elevation (Fang et al., 2009, Gao et al., 2013, Gou et al., 2005, Liang et al., 2016, Zhang et al., 2016, Zhang et al., 2011). To date, however, there has been only one investigation into the climate-growth patterns of Qinghai spruce in the Helan Mountains (Zhang et al., 2009). In that study, growth of Qinghai spruce is primarily limited by dry summers and cool December temperatures prior to the growing season. We do not know whether the Zhang et al. (2009) study represents the climate-growth relation of Qinghai spruce across its elevational distribution in the Helan Mountains.

Here, we investigate the potential climatic drivers of Qinghai spruce growth across its elevational distribution in the Helan Mountains. Specifically, we sampled Qinghai spruce at its upper, middle, and lower elevational distributional margins. As elevation increases in the mountains of northwest China, temperature decreases and precipitations increases (Domrös & Peng, 1988). Thus, our first hypothesis is that Qinghai spruce growth at its
upper distributional margin is significantly and positively correlated to temperature. Our second hypothesis is that Qinghai spruce’s growth at its lower margin in the Helan Mountains is significantly and positively correlated to moisture availability. For the second hypothesis, we consider a reduction in moisture to be expressed as a statistically significant positive correlation to precipitation and a statistically significant negative correlation to temperature, especially maximum temperatures.

**Materials and methods**

*Study site*

Our study region is located on the eastern side of the Helan Mountain, Ningxia Hui Autonomous Region, China (Fig. 1). The Helan Mountains region is also the northwestern extent of the East Asian Summer Monsoon (Zhang et al., 2009) and located at arid and semi-arid areas in Central Asia. There are two bands of coniferous forests across elevation within this region: one is dominated by Chinese pine (*Pinus tabulaeformis* Carr.) from 1900-2350 m elevation while the other one is dominated by Qinghai spruce from 2350-3100 m (Jiang et al., 2007). Meteorological data from the High Mountain meteorological station from 1961-1990 indicates that the mean annual temperature is -0.7 °C while the mean monthly growing season temperatures (May-September) are above 5 °C (Fig. 2). Annual total precipitation is 427 mm, 40% of which occurs during the peak of the monsoon season, from July to August. Overall, annual temperatures have been increasing while total annual precipitation has been relatively stable over time (Fig. 3). Variability in early growing season precipitation, e.g. May and June, has increased in recent decades.
**Figure 1.** Sample sites, meteorological stations, and Qinghai spruce spatial distribution (modified from Liu, 1992).

**Figure 2.** Climate diagrams (after Walter, 1979) from High Mountain (HM), Alxa Left Banner (ALB), and Yinchuan (YC) stations (locations are shown in Figure 1). Dashed lines
represent the mean monthly temperature, solid lines the mean monthly precipitation sum. Red areas correspond to relative dry periods and blue areas correspond to relatively humid periods.

Figure 3. Time series (solid lines) and linear trends (dash lines) of average annual temperature and total annual precipitation.

Tree-ring data

Increment cores of Qinghai spruce were collected from three sites along an elevation gradient, named the lower distributional margin (LDM), mid-distribution (MID), and upper distributional margin (UDM) sites respectively (Table 1). All sites were located on slopes of 15-25 degree. At each site, 25 mature and healthy-appearing canopy trees were selected for sampling. At least two cores were extracted from each tree at breast height (1.3m from the ground), though some trees had three or four cores extracted as coring occasionally went through the entire stem. Samples were dried, mounted, and sanded with progressive finer sand paper. Samples were visually cross-dated to identify locally-absent rings and
false rings where necessary (Stokes & Smiley, 1968). Ring widths were then measured to the nearest 0.01 mm using a LINTAB 5 measuring table (Rinntech, Heidelberg, Germany) with the accuracy of cross-dating was checked by program COFECHA (Holmes, 1983). Cores that were too rotten to accurately date were not used for this study.

**Table 1.** Characteristics of the sampling sites.

| Site | Latitude (° N) | Longitude (° E) | Elevation (m a.s.l.) | Main aspect | Slope (°) | No. trees/radii |
|------|----------------|-----------------|----------------------|-------------|-----------|----------------|
| UDM  | 38.77          | 105.90          | 2886                 | Northeast   | 25        | 25/78          |
| MID  | 38.77          | 105.90          | 2670                 | North       | 25        | 25/89          |
| LDM  | 38.78          | 105.90          | 2408                 | Northeast   | 15        | 25/90          |

To remove size-related trends in tree growth, most ring width series were detrended using negative exponential functions. Series with trends that indicated release from competition or other ecological processes were detrended using 30-year smoothing splines. Detrended series were prewhitened by autoregressive modeling to remove natural persistence due to climate and tree physiology (Cook, 1985). All individual standardized ring-width series from the same site were averaged into site-level chronologies using bi-weight robust mean (Cook, 1985). Similarly, standardized ring-width series from the same tree were averaged into single-tree chronologies. For our analysis, we used both the standard and residual chronology types (Cook, 1985). We used the standard chronologies for growth analyses and the residual chronologies for calculating the relationship between climate variables and radial increment.
Climate data

Meteorological data comes from three stations near the study area (Fig. 1): High Mountain (HM), Alxa Left Banner (ALB), and Yinchuan (YC). HM was the nearest station to the sample sites, but provided only 30-year data (1961-1990). ALB and YC both provided meteorological data from 1953 to present. Thus, the average annual values for HM were used to describe the climate of the study area while ALB and YC were used to describe the climate variation. Monthly data of maximum temperature, minimum temperature, precipitation, wind speed, hours of sunshine, relative humidity, and surface atmospheric pressure was used to estimate 1-month SPEI (SPEI-1) via the FAO56 Penman-Monteith method (Allen et al., 1998). Daily data of maximum temperature, minimum temperature, and relative humidity was used to estimate vapor pressure deficit (VPD, Allen et al., 1998). Daily VPD values were averaged to calculate monthly mean VPD. Monthly precipitation, minimum temperature, maximum temperature, SPEI-1, and VPD from ALB and YC were averaged to avoid single-station bias and reflect regional climate change conditions (Blasing et al., 1981).

Statistical analysis

Two statistics were used to estimate the potential climatic effect on tree growth, the standard deviation (SD) and the first-order autocorrelation coefficient. A higher SD suggests a stronger climatic influence on tree growth while a higher first-order autocorrelation coefficient suggests a stronger influence of tree growth from one year to the next (Cook, 1985). Both SD and first-order autocorrelation coefficient were calculated for the common intervals of all single-tree standard chronologies.
The limiting factors of radial growth were identified by correlation analysis. Pearson's correlation coefficients were calculated between single-tree residual chronologies and climate variables from 1954-2010. Climate factors included total monthly precipitation, monthly minimum, and monthly maximum temperature from previous May to current October to cover the growing season (May-September) of Qinghai spruce (Liang et al., 2006) and include lags due to non-structural carbon.

First-order autocorrelation coefficients and correlation coefficients was converted into a Z-score using Fisher's r-to-z transformation for comparing. One-way ANOVA followed by Tukey HSD test was used to test difference in tree age, diameter at breast height (DBH), SD, first-order autocorrelation coefficients and correlation coefficients between our three sites.

**Results**

*Occurrence of locally-absent rings*

The frequency of locally-absent rings is greater at the lower elevation (LDM) than at higher elevations (Table 2). Locally-absent rings occur in more years at LDM than at MID and UDM (12 versus 6 and 4 years, respectively). Even when the trees were younger, during 1940s for example, locally-absent rings were only documented at the LDM site. Of the trees with locally-absent rings in three or four radii, 95% are growing at the LDM. Nearly all LDM trees, 92%, have locally-absent ring in at least one radius over the lifetime of the tree, while 68% have locally-absent rings in at least two radii and 44% in at least three radii. In recent decades, high rates of locally-absent rings occurred in four years, 1982, 2001, 2005, and 2008. Again, the LMD site had the highest rate of locally-absent rings during
these years. The percentage of LMD trees with locally-absent rings during these years ranged from 48-84%, while the ranges for MID and UDM was 0-12% at each site. During these four years at LDM, 12-36% of trees had locally-absent rings in at least three radii.

**Table 2** Years with locally-absent rings since 1941.

| Year | Rate of trees with locally-absent rings in at least one radius |
|------|-------------------------------------------------------------|
|      | LDM  | MID  | UDM  |
| 1941 | 4    | 0    | 0    |
| 1947 | 8    | 0    | 0    |
| 1973 | 0    | 0    | 4    |
| 1981 | 8    | 0    | 4    |
| 1982 | 52   | 12   | 12   |
| 1991 | 12   | 0    | 4    |
| 1994 | 20   | 0    | 4    |
| 1995 | 4    | 0    | 4    |
| 2000 | 8    | 0    | 0    |
| 2001 | 60   | 4    | 0    |
| 2005 | 84   | 4    | 4    |
| 2006 | 24   | 4    | 0    |
| 2008 | 48   | 0    | 0    |

The rates of locally-absent rings seemed high for spruce trees (genus *Picea*). To understand if these rates are unusually high, we conducted an analysis of the rate of locally-absent rings of spruce archived in the International Tree-Ring Databank (https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring); we could not find rates of locally-absent rings of spruce in the St. George *et al.* (2013) review. Labeling of ITRDB samples made it hard to calculate the rate of locally-absent rings at the
tree level such that we calculated rates per radius per site for this analysis. We were also curious that the environmental conditions of the Helan Mountain Qinghai spruce made them unusual versus ITRDB spruce. To explore this possibility, we placed them in an elevational and latitudinal context. Of the 810 spruce sites in the ITRDB, 580 have both latitude and elevation information and 20 series or more (assuming to contain roughly 10-20 trees). The 580 sites were split into four groups – the lower 10% in latitude, top 10% in latitude, bottom 10% in elevation, and top 10% in elevation (Fig. S1). We found that the bottom 10% in latitude and the top 10% in elevation have higher rates of locally-absent rings and the Helan Mountain Qinghai spruce fall in the two geographic categories. Of collections in the ITRDB that appear to have an equal number of trees and radii sampled in our sites, only five collections have more locally absent rings than LDM (Fig. 4; Canada, latitude: 55.22 °N, elevation: 370 m; Canada, latitude: 67.70 °N, elevation: 267 m; Switzerland, latitude: 46.42 °N, elevation: 1250 m; Switzerland, latitude: 46.30 °N, elevation: 840 m; United States, latitude: 48.72 °N, elevation: 2141 m). Compared to these sites, LDM is lower in latitude (38.78 °N), but higher in elevation (2408 m).

![Figure 4](image-url)

**Figure 4.** Maximum rate of radii with locally-absent rings of spruce collections from the
ITRDB with 20 series or more versus our collections in the Helan Mountains (red squares). Boxplots depict the median (horizontal solid line), 25th and 75th percentiles (lower and upper edges of boxes), and 5th and 95th percentiles (whiskers) values.

Tree growth and age and size structure analysis

Mean tree age at LDM and UDM are slightly higher than that at MID (89 and 93 years versus 84 years, respectively; Fig. 5), but there is no significant difference in tree age between each location ($F = 1.769, p = 0.178$). Similarly, while mean DBH differ across sites (LDM: 21 cm, MID: 22 cm, UDM: 23 cm), there is no significant difference in average DBH ($F = 1.684, p = 0.193$).

Figure 5. Tree age, DBH, and characteristics of single-tree standard chronologies. Boxplots depict the median (horizontal solid line), 25th and 75th percentiles (lower and upper edges of boxes), and 5th and 95th percentiles (whiskers) values.
The standard chronologies have a similar amount of high frequency variation in radial growth across elevations (Fig. 6); they crossdate. There is, however, a significant difference of SD between the elevations sampled ($F = 115.8$, $p < 0.001$; Fig. 5). The mean SD at LDM is significantly higher than at MID and UDM (0.605 versus 0.415 and 0.390, respectively), indicating LDM trees could be more sensitive to climatic variation compared to the other locations. There is also a significant difference of first-order autocorrelation coefficients between the three elevations ($F = 56.19$, $p < 0.001$; Fig. 5). The mean first-order autocorrelation coefficient at LDM is nearly zero and significantly less than at MID and UDM (-0.025 versus 0.303 and 0.247 respectively). These values indicate that trees at LDM have a lower persistence structure (autocorrelation from one year to the next) and that climate variation potentially has a greater influence on annual tree growth at lower elevation. The variation of the LDM chronology has increased in recent decades (SD of the site-level standard chronology before 1989 is 0.276, and that after 1990 is 0.463).

**Figure 6.** Single-tree and site-level standard chronologies (gray and black lines respectively).
Climate-growth relationships

The correlations between climate and single-tree residual chronologies are similar between sites (Fig. 7). Generally, growth is positively correlated with total May and total June precipitation, and previous September, March, May, and July SPEI-1. Growth is also negatively correlated with average March and average July temperature, and average previous September, average March, average May, and average July VPD.

Figure 7. Correlations coefficients between climate and single-tree growth series from LDM (red), MID (green), and UDM (blue). Boxplots depict the median (horizontal solid line), 25th and 75th percentiles (lower and upper edges of boxes), and 5th and 95th
percentiles (whiskers) values of correlation coefficients. Dashed lines represent 95% significance levels.

Single-tree residual chronologies at LDM have significant higher correlation coefficients than those at MID and UDM for total May and total June precipitation. These same chronologies have significant lower correlation coefficients than those at MID and UDM for previous September VPD. High rates of locally-absent rings at LDM (50% and greater) are most strongly correlated with low June precipitation (Fig. 8). Years with rates of locally-absent rings higher than 25 cluster more tightly when both low June precipitation and high July VPD occur; that is, high July VPD helps to better account for climatic drivers of high rates of locally-absent rings.

**Figure 8.** Relationship between rate of trees with locally-absent rings in at least one radius at LDM and climatic variables most strongly related to radial growth. Note how the years
with high rates of locally-absent rings cluster as July VPD is added to June precipitation (lower right).

**Discussion**

*Cessation of stem growth in Qinghai spruce*

Three important findings here are that 1) the rate of locally-absent rings of Qinghai spruce was greater at the lower distributional margin site versus the two populations at higher elevation in the Helan Mountains despite all populations having a strongly similar structure in monthly climatic sensitivities, 2) the occurrence of severe, locally-absent ring events in canopy trees has increased since 2001, and 3) the lower distributional margin population in our study had one of the highest rates of locally-absent rings when compared to ITRDB spruce collections with a comparable sample replication. ‘Locally-absent ring’ is a dendrochronological term indicating that a tree had no visible growth in the sampled radius during a specific year and are identified through crossdating, a process of identifying the pattern of common large and small rings within a tree and then within a population of trees (Douglass, 1920, Fritts, 1976, Stokes & Smiley, 1968). The recent rates of locally-absent rings are near the highest rates for spruce locally and globally while only having a marginally different climatic sensitivity compared to local populations.

The temporary cessation of stem growth, or a locally-absent ring, is one way trees adjust to extreme climatic conditions. Extreme climate is not the only trigger of the temporary cessation of stem growth. Common factors of locally-absent rings include insect outbreaks (Alfaro et al., 1982), severe fire (Catry et al., 2010), the competitive stress placed on
understory trees by canopy trees (Lorimer et al., 1999), and earthquakes (Jacoby, 1997, Jacoby et al., 1988). Fire is rare in our study region, insects are not typically an ecological factor in these mountains, and the sampled Qinghai spruce trees are not on earthquake fault zone. Also, the trees we sampled were overstory trees, making it unlikely that overstory competition was a factor of locally-absent rings in recent decades. It is difficult to see how canopy position accounts for the differences in locally-absent ring rates between the lower distributional margin trees versus trees at higher elevation, especially when considering there was virtually no difference in the ages and diameters between all sites (indicating a similar stage of forest development between sites). We do not have measures of stand density but because tree sizes are so similar, it is reasonable to think stand densities are not greatly different. We cannot, however, rule out stand density as a factor in the differing rates between sites.

**Drought effects on tree growth**

We found that Qinghai spruce growth is sensitive to moisture conditions—low precipitation and high temperatures—across an elevation gradient in the Helan Mountains. This finding does not support our first hypothesis that northern distributional margin population, the population at the highest elevation, would be limited by cool temperatures. Climatic-sensitivity analyses do support our second hypothesis, that lower distributional margin populations are limited by reduced moisture availability. The effect of low growing-season precipitation on the populations of Qinghai spruce we sampled on Helan Mountain support the relation between climate and Qinghai spruce growth over much of its distribution (e.g. Gao et al., 2013, Gou et al., 2005, Liang et al., 2010, Zhang et al., 2016). Only at a few extremely high elevations does warming enhance
Qinghai spruce growth (Chen et al., 2012). We are not yet sure if these relations between low precipitation and high temperatures in Helan Mountain Qinghai spruce are consistent through time. A study investigating a changing climatic sensitivity is an important next step in this line of research.

An important aspect of future research would be to examine the subtle and virtually nonlinear impact of moisture conditions on Qinghai spruce growth over elevation on Helan Mountain. Even though each population had the same basic climatic response, strength of chronology statistics (SD, first-order autocorrelation coefficients), and calculated climatic sensitivity, the differences, while smaller, were large moving from the lower elevation than from the mid to upper elevation. The importance of the small differences between lower and upper elevation populations appear great: the rate of locally-absent rings at LMD are significantly greater when compared to mid- and upper-distribution populations. That increased moisture improves growth more from lower boundary to interior of Qinghai spruce forest than when moving upslope follows a general phenomenon in dendroecological studies (Cernusak & English, 2015). This is still, however, an active line of research. European beech, for example, appears to be more vulnerable to climate in the middle of its range in central Europe versus range margins (Cavin & Jump, 2016, Hacket-Pain et al., 2016).

Implications of Qinghai spruce growth and climatic sensitivity

Locally-absent rings or the temporary cessation of stem growth is an important ecological signal. While it is not possible to extrapolate these events across the stem from the radii sampled, a high frequency of locally-absent rings can signal a potential increase in the stress level of trees. In fact, an increase in the frequency of locally-absent rings is
sometimes found prior to a decline in radial growth or tree mortality (Cailleret et al., 2016, Liang et al., 2016). Because the LMD trees had the highest rate of locally-absent rings, rates have increased in that population over the last two decades, and that three of the four most severe events have occurred since 2001, we conclude that this population has become more stressed over the last two decades.

Based on 1961-1990 averages from the HM meteorological station, May through July total potential evapotranspiration often approaches total precipitation (162.2 mm of total potential evapotranspiration via the Thornthwaite method versus 165.6 mm of total precipitation). Thus, when reduced rainfall or increased maximum temperatures occur, it is likely that soil water is not sufficient for photosynthesis. In fact, during the four years with the most intense locally-absent ring events (1982, 2001, 2005, and 2008), total June precipitation was 0.7-1.3 SD below the mean (Fig. 8). In 2005, when 84% of the sampled trees had at least one locally-absent ring, total June precipitation was 1.3 SD below the mean. The evidence that we have indicates that low precipitation in June, just prior to the peak in monsoonal precipitation, is likely the most common trigger of increasing locally-absent ring events since 2001.

To date, there has been little to no trend in the amount of precipitation within the distribution of Qinghai spruce. Changing temperatures, however, could have increased the severity of drought within the region in recent decades. Warming is expected to increase dry conditions globally over the next several decades (Cook et al., 2014). Temperature has significantly increased across the distribution of Qinghai spruce since 1960 (Piao et al., 2010), resulting in increased potential evapotranspiration, reduced soil moisture, and an increase in soil drought events (Wang et al., 2011). These changes can impact tree growth
in two ways. First, growth declines or ceases during severe drought. Second, plants in arid areas need several years to recover from drought events (Anderegg et al., 2015). Thus, the increase in precipitation variation and an accompaniment warming could be increasing the moisture stress on Qinghai spruce. In fact, we have found that increased vapor pressure deficit in July is an important additional factor in the cessation of stem growth of Qinghai spruce in the Helan Mountains (Fig. 8).

We hypothesize that increased warming without a substantial increase in precipitation would induce a significant decline in growth and, possibly, an increase in mortality of lower distribution Qinghai spruce in the Helan Mountains. Similar findings have been observed in other semi-arid forests (Settele et al., 2015, and references within). It is hard to predict how the Qinghai spruce forest on the Helan Mountains might change under future conditions. It might be that other species increase in importance during warming as these species become a better overall competitor versus Qinghai spruce at lower elevations. If so, the community structure could change, resulting in a narrowed elevational distribution of Qinghai spruce. Within the entire distribution of Qinghai spruce, however, there is substantial uncertainty around this potential trajectory of forest development. For example, Qinghai spruce in the Qilian Mountains has more locally-absent rings at upper and middle elevations than lower elevations. Difference in canopy cover and stem density appear to be at work in the Qilian Mountain populations (Liang et al., 2016). At the very least, our results in this study fall in line with observations that extreme heat and drought events reduce primary productivity (Ciais et al., 2005), suggesting that an increase in extremely hot years or severe drought will reduce the ability of the Qinghai spruce forest on the Helan Mountains to act as a carbon sink.
We found that the growth of Qinghai spruce across elevation in the Helan Mountains of northwest China is driven by moisture conditions. Trees at a lower distributional margin, however, are more sensitive to reduced precipitation than those at higher elevations and have experienced a significant increase in stem-growth cessation in recent decades versus populations at higher elevations. A significant reduction in early-monsoonal precipitation appears to the primary cause of cessation in stem growth. Increased July vapor pressure deficit appears to exacerbate stem-growth cessation in lower distributional margin trees. In other types of ecosystems, it has been shown that stem-growth cessation often precedes increased rates of tree mortality. If future environmental conditions deteriorate, climatic change could become a threat to the endemic Qinghai spruce on the Helan Mountains.

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Reference

Alfaro RI, Sickle GaV, Thomson AJ, Wegwitz E (1982) Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. Canadian Journal of Forest Research, 12, 780-787.

Allen RG, Pereira LS, Raes D, Smith M (1998) Crop evapotranspiration - Guidelines for computing crop water requirements. pp Page, Rome, Italy, Food and Agriculture Organization of the United Nations.
Anderegg WRL, Schwalm C, Biondi F et al. (2015) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science, 349, 528-532.

Bhuta AaR, Kennedy LM, Pederson N (2009) Climate-radial growth relationships of northern latitudinal range margin longleaf pine (Pinus palustris P. Mill.) in the Atlantic coastal plain of southeastern Virginia. Tree-Ring Research, 65, 105-115.

Blasing TJ, Duvick DN, West DC (1981) Dendroclimatic calibration and verification using regionally averaged and single station precipitation data. Tree-ring bulletin, 1981, 37-43.

Boisvert-Marsh L, Périé C, De Blois S (2014) Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. Ecosphere, 5, 1-33.

Cailleret M, Jansen S, Robert EMR et al. (2016) A synthesis of radial growth patterns preceding tree mortality. Global Change Biology.

Catry FX, Rego F, Moreira F, Fernandes PM, Pausas JG (2010) Post-fire tree mortality in mixed forests of central Portugal. Forest Ecology and Management, 260, 1184-1192.

Cavin L, Jump AS (2016) Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree Fagus sylvatica L. not the equatorial range edge. Global Change Biology.

Cernusak LA, English NB (2015) Beyond tree-ring widths: stable isotopes sharpen the focus on climate responses of temperate forest trees. Tree physiology, 35, 1-3.

Chen F, Yuan Y-J, Wei W-S et al. (2012) Temperature reconstruction from tree-ring maximum latewood density of Qinghai spruce in middle Hexi Corridor, China. Theoretical and Applied Climatology, 107, 633-643.

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science, 333, 1024-1026.
Chhin S, Wang GG, Tardif J (2004) Dendroclimatic analysis of white spruce at its southern limit of distribution in the Spruce Woods Provincial Park, Manitoba, Canada. Tree-Ring Research, 60, 31-43.

Ciais P, Reichstein M, Viovy N et al. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature, 437, 529-533.

Cook BI, Smerdon JE, Seager R, Coats S (2014) Global warming and 21st century drying. Climate Dynamics, 43, 2607-2627.

Cook ER (1985) A time series analysis approach to tree ring standardization. Unpublished Ph.D. University of Arizona, Tucson, Arizona, USA.

Cook ER, Nance WL, Krusic PJ, Grissom J (1998) Modeling the differential sensitivity of loblolly pine to climatic change using tree rings. In: The productivity and sustainability of southern forest ecosystems in a changing environment. (eds Mickler RA, Fox S) pp Page. New York, NY, Springer New York.

D’orangeville L, Duchesne L, Houle D, Kneeshaw D, Côté B, Pederson N (2016) Northeastern North America as a potential refugium for boreal forests in a warming climate. Science, 352, 1452-1455.

Domrös M, Peng G (1988) The climate of China, Springer-Verlag Berlin Heidelberg.

Douglass AE (1920) Evidence of climatic effects in the annual rings of trees. Ecology, 1, 24-32.

Dulamsuren C, Hauck M, Leuschner HH, Leuschner C (2011) Climate response of tree-ring width in Larix sibirica growing in the drought-stressed forest-steppe ecotone of northern Mongolia. Annals of Forest Science, 68, 275-282.

Fang K, Gou X, Levia DF et al. (2009) Variation of radial growth patterns in trees along
three altitudinal transects in north central China. Iawa Journal, 30, 443-457.

Fritts HC (1976) *Tree rings and climate*, London, Academic Press.

Galván JD, Camarero JJ, Gutiérrez E, Zuidema P (2014) Seeing the trees for the forest: drivers of individual growth responses to climate in *Pinus uncinata* mountain forests. Journal of Ecology, 102, 1244-1257.

Gao L, Gou X, Deng Y, Yang M, Zhao Z, Cao Z (2013) Dendroclimatic response of *Picea crassifolia* along an altitudinal gradient in the eastern Qilian Mountains, northwest China. Arctic, Antarctic, and Alpine Research, 45, 491-499.

Gou X, Chen F, Yang M, Li J, Peng J, Jin L (2005) Climatic response of thick leaf spruce (*Picea crassifolia*) tree-ring width at different elevations over Qilian Mountains, northwestern China. Journal of Arid Environments, 61, 513-524.

Hacket-Pain AJ, Cavin L, Friend AD, Jump AS (2016) Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European beech indicates widespread vulnerability to changing climate. European Journal of Forest Research, 135, 897-909.

Hilasvuori E, Berninger F (2010) Dependence of tree ring stable isotope abundances and ring width on climate in Finnish oak. Tree physiology, 30, 636-647.

Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. Tree-ring bulletin, 43, 69-78.

Housset JM, Girardin MP, Baconnet M, Carcaillot C, Bergeron Y (2015) Unexpected warming-induced growth decline in *Thuja occidentalis* at its northern limits in North America. Journal of Biogeography, 42, 1233-1245.

Jacoby GC (1997) Application of tree ring analysis to paleoseismology. Reviews of
Jacoby GC, Sheppard PR, Sieh KE (1988) Irregular Recurrence of Large Earthquakes along the San Andreas Fault: Evidence from Trees. Science, **241**, 196-199.

Jiang Y, Kang M, Zhu Y, Xu G (2007) Plant biodiversity patterns on Helan Mountain, China. Acta Oecologica, **32**, 125-133.

Kharuk VI, Im ST, Oskorbin PA, Petrov IA, Ranson KJ (2013) Siberian pine decline and mortality in southern siberian mountains. Forest Ecology and Management, **310**, 312-320.

Lesica P, Mccune B (2004) Decline of arctic-alpine plants at the southern margin of their range following a decade of climatic warming. Journal of Vegetation Science, **15**, 679-690.

Liang E, Eckstein D, Liu H (2008) Climate-growth relationships of relict Pinus tabulaeformis at the northern limit of its natural distribution in northern China. Journal of Vegetation Science, **19**, 393-406.

Liang E, Leuschner C, Dulamsuren C, Wagner B, Hauck M (2016) Global warming-related tree growth decline and mortality on the north-eastern Tibetan plateau. Climatic Change, **134**, 163-176.

Liang E, Shao X, Eckstein D, Huang L, Liu X (2006) Topography- and species-dependent growth responses of Sabina przewalskii and Picea crassifolia to climate on the northeast Tibetan Plateau. Forest Ecology and Management, **236**, 268-277.

Liang E, Shao X, Eckstein D, Liu X (2010) Spatial variability of tree growth along a latitudinal transect in the Qilian Mountains, northeastern Tibetan Plateau. Canadian Journal of Forest Research, **40**, 200-211.
Liu X (1992) *Qinghai spruce*, Lanzhou, China, Lanzhou University Press.

Lloyd AH, Bunn AG, Berner L (2011) A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. Global Change Biology, 17, 1935-1945.

Lorimer CG, Dahir SE, Singer MT (1999) Frequency of partial and missing rings in *Acer saccharum* in relation to canopy position and growth rate. Plant Ecology, 143, 189-202.

Martin-Benito D, Pederson N (2015) Convergence in drought stress, but a divergence of climatic drivers across a latitudinal gradient in a temperate broadleaf forest. Journal of Biogeography, 42, 925-937.

Pederson N, Cook ER, Jacoby GC, Peteet DM, Griffin KL (2004) The influence of winter temperatures on the annual radial growth of six northern range margin tree species. Dendrochronologia, 22, 7-29.

Peñuelas J, Hunt JM, Ogaya R, Jump AS (2008) Twentieth century changes of tree-ring δ¹³C at the southern range-edge of *Fagus sylvatica*: increasing water-use efficiency does not avoid the growth decline induced by warming at low altitudes. Global Change Biology, 14, 1076-1088.

Piao S, Ciais P, Huang Y *et al.* (2010) The impacts of climate change on water resources and agriculture in China. Nature, 467, 43-51.

Settele J, Scholes R, Betts RA *et al.* (2015) Terrestrial and inland water systems. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change*. (eds Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL) pp Page.
Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press.

Shi J, Cook ER, Lu H, Li J, Wright WE, Li S (2010) Tree-ring based winter temperature reconstruction for the lower reaches of the Yangtze River in southeast China. Climate Research, 41, 169-175.

St. George S, Ault TR, Torbenson MCA (2013) The rarity of absent growth rings in Northern Hemisphere forests outside the American Southwest. Geophysical Research Letters, 40, 3727-3731.

Stokes MA, Smiley TL (1968) An introduction to tree-ring dating, University of Arizona Press.

Tardif JC, Conciatori F, Nantel P, Gagnon D (2006) Radial growth and climate responses of white oak (Quercus alba) and northern red oak (Quercus rubra) at the northern distribution limit of white oak in Quebec, Canada. Journal of Biogeography, 33, 1657-1669.

Urli M, Lamy J-B, Sin F, Burlett R, Delzon S, Porté AJ (2015) The high vulnerability of Quercus robur to drought at its southern margin paves the way for Quercus ilex. Plant Ecology, 216, 177-187.

Walter H (1979) Vegetation of the earth and ecological systems of the geo-biosphere, New York, Springer-Verlag.

Wang A, Lettenmaier DP, Sheffield J (2011) Soil Moisture Drought in China, 1950–2006. Journal of Climate, 24, 3257-3271.

Zhang L, Jiang Y, Zhao S, Kang X, Zhang W, Liu T (2016) Lingering response of radial growth of Picea crassifolia to climate at different altitudes in the Qilian Mountains, Northwest China. Trees, 1-11.
Zhang Y, Shao X, Wilmking M (2011) Dynamic relationships between Picea crassifolia growth and climate at upper treeline in the Qilian Mts., Northeast Tibetan Plateau, China. Dendrochronologia, 29, 185-199.

Zhang Y, Wilmking M, Gou X (2009) Changing relationships between tree growth and climate in Northwest China. Plant Ecology, 201, 39-50.