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Warming induced growth decline of Himalayan birch at its lower range edge in a semi-arid region of Trans-Himalaya, central Nepal

Achyut Tiwari · Ze-Xin Fan · Alistair S. Jump · Zhe-Kun Zhou

Abstract Changes in the position of altitudinal treelines and timberlines are considered useful indicators of climatic changes on tree growth and forest dynamics. We sought to determine if recent warming is driving contrasting growth responses of Himalayan birch, at moist treeline (Lete Lekh) and semi-arid timberline (Chimang Lekh) sites in the Trans-Himalayan zone of central Nepal. We used dendrochronological techniques to measure tree ring width (TRW) and basal area increment (BAI) of birch trees from climatically contrasting but nearby sites.

The TRW series were correlated with climate records from nearby meteorological stations, and BAI was compared between populations to explore growth trends over recent decades. We found contrasting precipitation trends between nearby sites such that the wet site (Lete) is getting warmer and wetter, and the dry site (Chimang) is getting warmer and drier in recent decades. The radial growth of birch in both moist and semi-arid sites are positively correlated to spring (March–May) rainfall, and negatively correlated to mean and maximum temperature for the same period. The growth climate analysis indicated that moisture availability in early growing season is crucial

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for birch growth at these locations. The BAI of birch is declining more rapidly at the dry timberline than at the moist treelines in the recent decades, indicating that climatic warming might negatively impact birch radial growth where warming interacts with increasing spring drought in the region. Our work highlights contrasting growth response of birch to climate change at moist and semi-arid forests indicating that local climatic variation must be accounted for when assessing and forecasting regional patterns of tree growth in topographically complex regions like Trans-Himalaya, in order to make accurate predictions of vegetation responses to climate change.

Introduction

Mountains provide habitats for a large portion of the world's biodiversity (Beniston 2003). High mountain species are potentially most threatened under ongoing climate change because of their narrow distribution range, geographical isolation and unique ecological adaptations (Grabherr et al. 1994; La Sorte and Jetz 2010). Besides being susceptible to the impacts of a rapidly changing climate (Xu et al. 2009; Sharma and Tsering 2009; Aryal et al. 2012), mountains also provide valuable locations for the early detection of climatic change and its impacts on ecological and hydrological systems (Beniston 2003; Nogués-Bravo et al. 2007).

Temperature is usually the main limiting factor for tree growth in poleward and high-altitude treelines (Körner 2003; Holtmeier and Broll 2007; Harsch et al. 2009). Air and soil temperatures as well as topographic sheltering are important determinants of spatial patterns of tree seedling establishment at high altitude (Greenwood et al. 2014). Trees are, therefore, expected to increase growth and shift poleward and upward with warming temperatures and increased atmospheric CO_2 concentration (Körner 2000; Borgaonkar et al. 2011; Gaire et al. 2014, 2016). However, this expectation only holds true if there are no other factors limiting growth at species distributional limits in these regions. Tree growth in high mountains could also be impaired by increases in temperature, mostly

due to warming-induced water deficit (Cook et al. 2003; Sano et al. 2005; Lv and Zhang 2012; Yang et al. 2013; Dawadi et al. 2013; Liang et al. 2014; Qi et al. 2015; Tiwari et al. 2016; Gaire et al. 2016). Furthermore, in topographically complex regions such as the Trans-Himalayan zone of Nepal, rain shadow effects can lead to strong gradients of precipitation and drought stress over short distances, resulting in contrasting local limitations of tree growth and complicating prediction of regional changes (Schickhoff 2005; Schickhoff et al. 2015).

Tree ring width indices have proved to be useful proxies for growth climate interpretation, however, detrended ring width series retains less ecological and historical information such as forest disturbance, acute growth stress, and other low-frequency signals (Esper et al. 2002). Hence, unstandardized basal area increment (BAI) is often used as a more informative measure of tree growth trends in terms of total biomass production, than ring width measurements alone (Phipps and Whiton 1988; Peñuelas et al. 2011). Climatic warming, increased concentration of atmospheric CO_2, and associated changes to water-use efficiency are predicted to enhance tree growth across many species and regions (Morison, 1993; Morgan et al. 2004; Norby et al. 2005). However, such anticipated positive growth trends have not been observed in many parts of the world (Peñuelas et al. 2011). Rather, tree growth has locally declined, with the potential for increasing levels of mortality due to warming-induced drought (Jump et al. 2006; Peñuelas et al. 2007; Allen et al. 2010). Hence, quantifying interannual responses of tree growth to local variation in climate is an important approach to understand tree growth patterns and forest productivity (Bunn et al. 2005; Yang et al. 2010) in climate sensitive high-elevation forests.

Himalayan birch (*Betula utilis*) typically forms the treeline in many parts of Himalaya (Miehe et al. 2015), but its growth across the various climatic zones and complex topography of central Nepal is poorly explored. The treeline is generally considered as the highest elevation at which a single upright tree with height greater than 2 m is found over the landscape (Hofgaard 1997; Körner 2003), and alpine timberlines represent the upper limit of closed mountain forest with tree density (trees >5 m tall) of at least 30% coverage (Wardle 1974; Holtmeier 2003). Trees typically show contrasting growth responses to

warming temperatures at their upper and lower range edges (Peñuelas et al. 2008; Cavin and Jump 2016). However, differences in water availability might strongly modify expected responses to temperature. Consequently, we sought to determine the response of birch growth at its upper and lower range edge in high mountain forests which are subject to a contrasting moisture regime. Consequently, we set out to test expectations that the birch treeline should advance in areas with greater water availability (Schickhoff et al. 2015), and retreat in dry sites (Liang et al. 2014) despite general predictions of upward elevational shifts of mountain forest distributions (Harsch et al. 2009). Improving our understanding of local climate variability and its impact on tree growth and forest productivity is of high importance for our ability to predict spatial patterns of forest change and their consequences. Consequently, in this study, we hypothesized that elevated temperatures would have a greater negative impact on tree growth in dry versus wet high-altitude sites for *B. utilis*. We used tree ring records of *B. utilis* from contrasting climatic zones in the Trans-Himalayan region to (1) determine the limiting climatic factors for growth of *B. utilis* in moist and dry sites and (2) assess the growth trends of *B. utilis* at its upper and lower range edge with response to ongoing climate change.

Methods

Study area

This work was conducted at Lete Lekh (28.6°N, 83.58°E, 3650–3900 m asl) and Chimang Lekh (28.75°N, 83.7°E, 3000–3300 m asl) of Mustang district in the Trans-Himalayan zone of central Nepal. Lete Lekh is a relatively moist area with alpine birch treeline in the north east facing slope, whereas Chimang Lekh is a semi-arid zone with birch timberline in the south–west facing slope. Lete treeline is the upper treeline and the Chimang timberline is the lower range edge of *B. utilis* in the southern part of Mustang District; however, at Chimang, the birch treeline reaches as high as 4000 m asl only in the sheltered north-facing slopes (personal observation). The sites are characterized by a contrasting precipitation regime within a short distance, and lie within the Annapurna

Conservation Area (ACA). The Trans-Himalayan zone of central Nepal lies in the rain shadow formed by surrounding high mountains, where runoff water from snow cover is the main source of water (Aryal et al. 2012). The northern part of the Mustang lies in the Trans-Himalayan semi-arid dry zone, further north, the Tibetan type highland forms the driest zone of Nepal (Lomanthang: 200 mm annual rainfall) (Stainton 1972; Schickhoff 2005). The forested areas are thus confined to the southern part of the district covering only about 3.24% of land area (Government of Nepal 2010).

Species

Himalayan birch (*Betula utilis* D. Don) is a moderate-sized (<20 m tall) broadleaved pioneer tree species dominating an extensive area of subalpine forests up to 4500 m elevation, quite close to glaciers on northern slopes of the inner Himalayas (Stainton 1972; Zobel and Singh 1997; TISC 2002; Schickhoff 2005; Miehe et al. 2015). This species shows high variation in its local distribution possibly due to the influence of local-scale climate variability and topographic sheltering.

Field sampling

Field sampling was conducted during September–October of 2014 along transects on a topographically uniform area of the treeline at Lete and timberline at Chimang. Tree cores were collected from trees occurring in two treeline transects MT1 and MT2, each of which was 20 m × 120 m (hereafter MT for indicating moist treelines), and the third transect from a single timberline transect of 30 m × 50 m at Chimang (hereafter DT). The treeline sites included the treeline ecotone of *B. utilis* spanning the treeline and timberline.

We employed dendrochronological techniques for radial growth measurement and developing ring width chronology of trees. Single, two, or three cores were extracted from a tree using a 5.5 mm increment borer. All treeline trees were cored at the base of the tree (<30 cm), whereas DT trees were cored at breast height level. Tree cores were air-dried, mounted on sample holders, and sanded using progressively finer sandpaper according to standard methods (Fritts

1976). Ring widths were measured at a resolution of 0.01 mm with a LINTAB II measuring system (Rinntech Germany). Statistical analyses were performed using the software R (R Core Team 2015).

Meteorological data

Each study site has a meteorological station nearby (<4 km); however, the wet (Lete) site (28.63°N, 83.6°E, 2384 m asl) does not have temperature data for more than 15 years. The 15 years mean temperature of Lete was compared with temperature of Thakmarpha station (28.75°N, 83.7°E, 2566 m asl) for the same period and showed high correlation ($r = 0.69$, $n = 15$); hence, we used the Thakmarpha (1970–2013 AD) temperature records, and rainfall records of Lete and Chimang separately for growth climate analysis. The meteorological data showed mean annual rainfall of 1340 mm at Lete and 393 mm at Thakmarpha with mean annual temperature of 11.17 °C (Fig. 1).

Growth–climate response

Tree ring width (TRW) indices were employed to explore growth response to climate. We adopted visual inspection for cross-dating tree cores (Stokes and Smiley 1968), with statistical tests (sign-test and t test) using the software package TSAP-Win (Rinn 2003). Ring width measurements were detrended with a negative exponential using ARSTAN software (Cook 1985). We produced a standard tree ring width
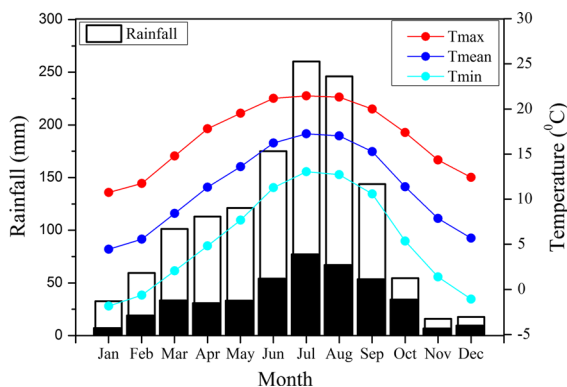

Fig. 1 Climate summary of Lete (2384 m asl) and Thakmarpha (2566 m asl) climate station (1970–2013 AD), the *white* and *black bars* represent the rainfall at Lete and Thakmarpha, respectively

chronology of 107 years using 56 tree cores from 52 trees at MT1, 186 years using 27 tree cores from 23 trees at MT2, and of 122 years using 49 tree cores from 24 trees at DT (Table 1). To maintain a reasonable sample depth, we limit the tree ring width chronology to the period representing a minimum of ten cores for each site. Growth–climate relationships were determined by correlating site standard chronology with monthly climatic variables (total rainfall, mean air temperature) from June of the previous growth year until October of the current growth year (Fritts 1976). Given the previously identified importance of spring season (March–May) moisture sensitivity of birch for high-elevation birch populations in the central Himalaya (Dawadi et al. 2013; Liang et al. 2014; Gaire et al. 2016), we also correlated the site chronology with mean climate for the March–May period.

Basal area index (BAI) chronology

BAI is commonly used to assessing tree and stand growth since it allows accurate quantification of tree productivity (Rubino and McCarthy 2000; Peñuelas et al. 2011). The BAI sigmoidal growth model is an appropriate means for detecting changes in tree growth avoiding detrending and standardizing employed in calculation of RWI (Phipps and Whiton 1988; Esper et al. 2002; Salzer et al. 2009). Here we used individual tree BAI to produce mean unstandardized BAI series across all trees at each site for each year.

Ring width was converted into tree BAI according to the following standard formula:

$$BAI = \pi \left(R_n^2 - R_{n-1}^2 \right),$$

where 'R' is the radius of the tree and 'n' is the year of tree ring formation. The BAI chronology was produced using the bai.out function in the dplR package in R as some tree cores had missed pith and almost every core had intact bark (R Core Team 2015). We produced BAI series from each site from the period which has at least 10 trees to represent the site population, and to avoid idiosyncrasies at the individual tree level. We analyzed the trend of BAI series at each site for the time period of 1990–2014 AD, that represented the growth trend after the growth release phase, thereby avoiding periods of juvenile growth

Table 1 Tree ring chronology summary statistics

Sampled location	Elevation range (m asl)	Chronology (years)	Mean series Length	No of cores (trees)	Mean sensitivity	EPS	All series Rbar	1st order AC
Moist treeline (MT1)	3650–3900	186	73	27 (23)	0.382	0.907	0.226	0.062
Moist treeline (MT2)	3700–3900	107	65	56 (52)	0.324	0.954	0.415	0.026
Timberline dry (DT)	3000–3300	122	79	49 (24)	0.360	0.968	0.315	0.001

EPS expressed population signal, *AC* autocorrelation

that are likely to be substantially determined by competitive interactions rather than climate (Jump et al. 2006).

Results

Climatic trends

Mustang (Lete and Thakmarpha) showed significant warming with a consistent increase of mean and maximum annual temperature during recent decades but without any trend in minimum temperatures (Fig. 2). The moist site (Lete) showed a significant increase in annual rainfall and a stable trend of spring season (March–May) rainfall, whereas the dry site (Thakmarpha) showed no rainfall trend. Hence, considering the overall balance of temperature trends and total rainfall, the moist site (MT) is getting wetter and

warmer whereas the dry site (DT) is getting drier and warmer in the recent decades (Figs. 2, 3a, b). The amount and duration of snow cover is an important determinant of soil moisture in high mountains in Himalayas (Müller et al. 2016). While we do not have direct measurements of snow cover at each study site, local people report substantial decrease in snow fall around Chimang (Tiwari, 2015 personal communication) (Fig. 4).
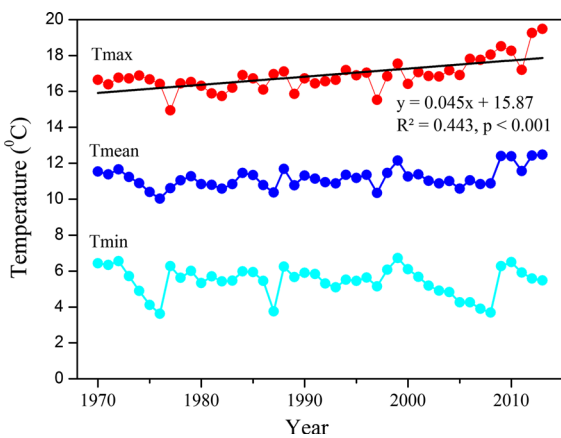

Fig. 2 Annual temperature trend of Thakmarpha (Mustang); maximum temperature (T_{max}), mean temperature (T_{mean}), and minimum temperature (T_{min})
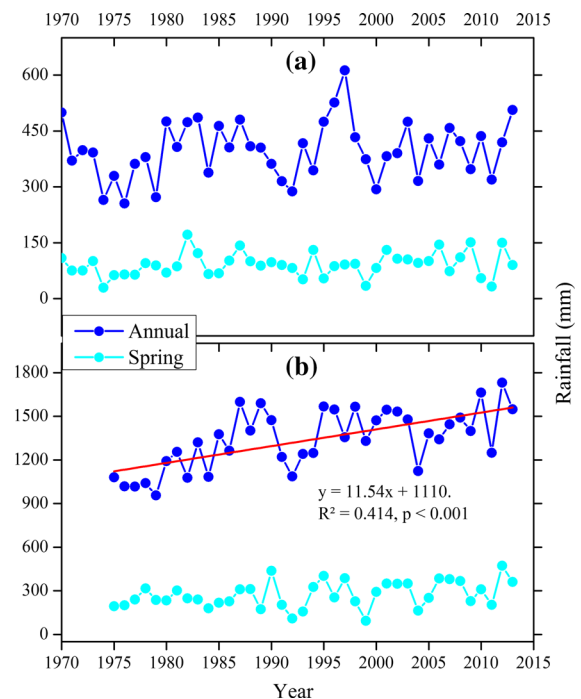

Fig. 3 Rainfall trend; total annual rainfall and total spring season (March–May) rainfall; **a** MT, **b** DT
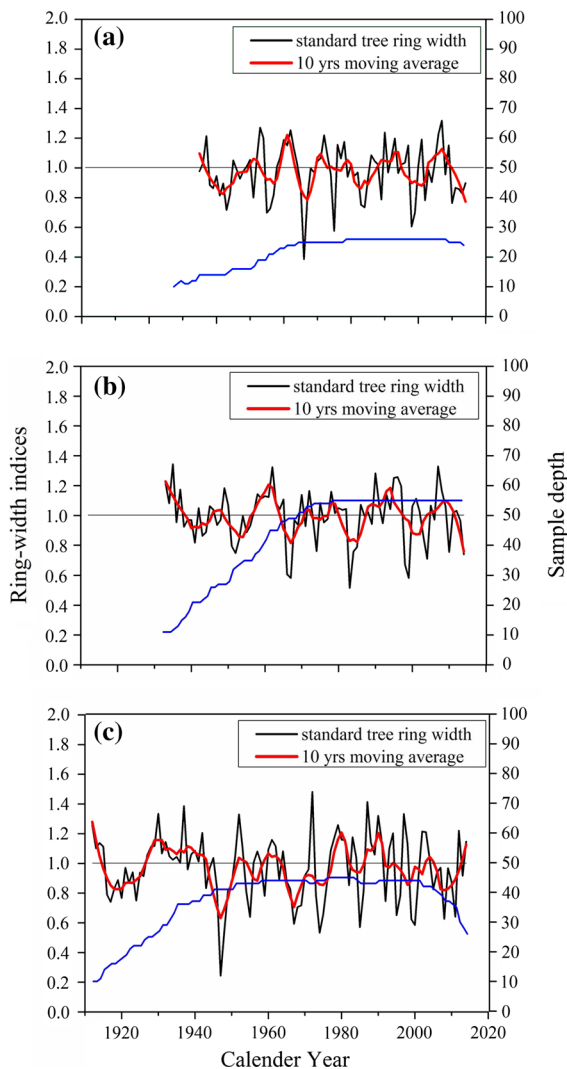
Fig. 4 Tree ring width standard chronology of *B. utilis*; **a** MT1, **b** MT2, **c** DT

Ring width chronology and growth–climate response

We produced three well-replicated tree ring with chronologies of *Betula utilis,* from the moist treeline sites, and semi-arid timberline site. The location of sampling sites and chronology statistics are summarized in Table 1.

The growth climate analysis of *B. utilis* revealed a significant positive relationship ($p < 0.05$) between the ring width series and monthly rainfall during spring season (March–May) both at moist treeline (MT1, MT2) and dry timberline (DT) (Fig. 5d–f). At least 1 month during spring season showed significant positive correlation ($p < 0.05$) of total rainfall with ring width indices in each site. Previous year's summer rainfall was found to have a stronger positive impact on tree radial growth at DT, while this effect was observed more weakly at MT1 and MT2. A significant negative relationship ($p < 0.05$) between radial growth and mean temperature (T_{mean}) for the spring season was observed at both treeline sites (MT1 and MT2), although this relationship was weaker at DT. T_{mean} of October also showed a significant negative relationship with radial growth ($p < 0.05$) at MT1 and DT (Fig. 5a, c). Further, the minimum temperature (T_{min}) showed stronger negative correlation in early growing season (Feb–May) at MT2, which was weaker at MT1 and DT. However, the maximum temperature (T_{max}) showed stronger negative correlation to ring width indices at DT in comparison to MT1 and MT2. Overall, while similarities in response are clear, we also found a contrasting response of radial growth to monthly climate among sites.

Temporal pattern of radial growth

BAI chronology at MT1 (1933–2014) and MT2 (1935–2014 AD) indicated a rapid increase followed by relatively stable (MT1) and weakly declining (MT2) trend in recent years, whereas at DT, BAI (1912–2014 AD) increased steadily at the beginning and declined abruptly in recent decades. BAI at DT showed a statistically significant declining trend, while that of MT1 and MT2 was without statistically significant trend for the same period (1990–2014 AD) as indicated by linear regression (Figs. 6, 7).

Discussion

Climatic trends

Climate data for the study regions at Mustang showed a consistent warming both at MT and DT, and high spatial variability in rainfall, as reported in Eastern Himalayas (Sharma et al. 2000; Shrestha et al. 2012). The moist region of Lete is getting wetter and warmer with increasing rainfall, whereas the semi-arid region of Thakmarpha is getting drier and warmer with very low and stable rainfall over recent decades. Such
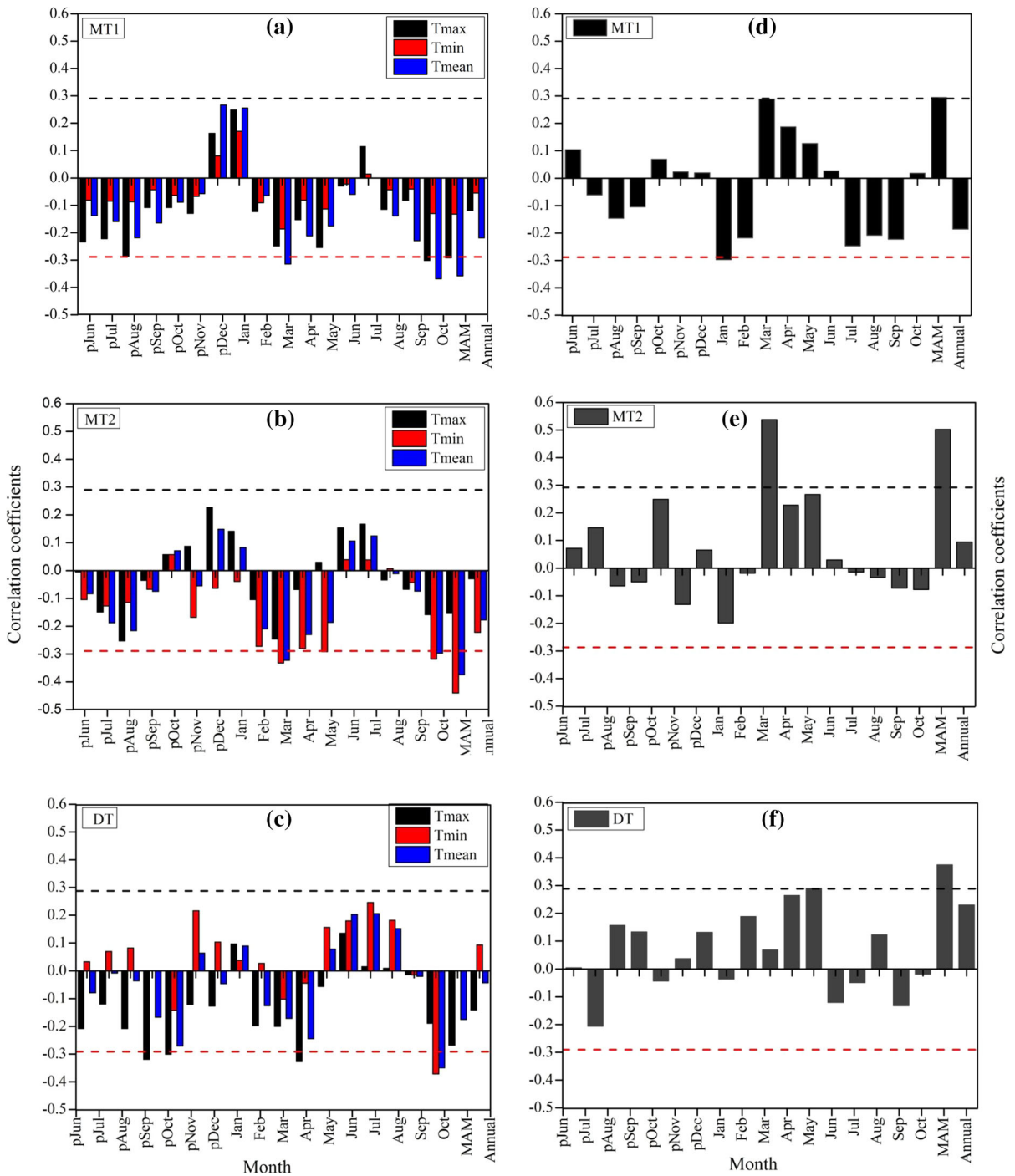
Fig. 5 Correlation coefficients of tree ring width indices, with total monthly maximum (T_{max}), mean (T_{mean}), and minimum temperature (T_{min}); MT1 (**a**), MT2 (**b**), DT (**c**), and total monthly rainfall; MT1 (**d**), MT2 (**e**), DT (**f**); of June in the previous year to October of the current year, spring season and annual climate, *dashed horizontal lines* indicate significant correlation at 95% confidence limit for a two-tailed test
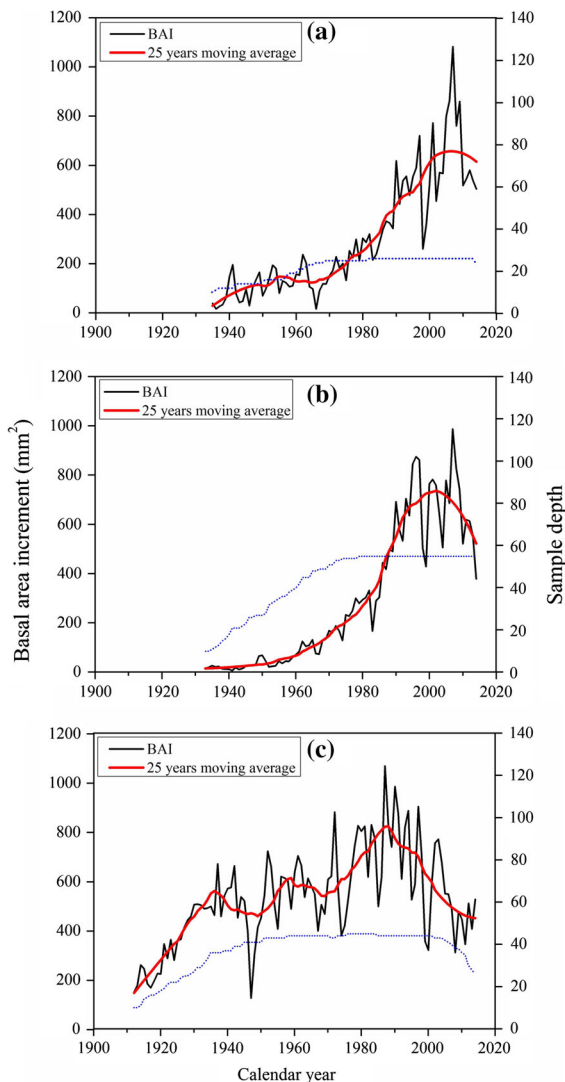
Fig. 6 Basal area increment (BAI) chronology of *B. utilis* at moist treeline; MT1 (**a**), MT2 (**b**), dry timberline DT (**c**)

Fig. 7 BAI trend during 1990–2014 AD at MT1 (**a**), MT2 (**b**) and DT (**c**), *solid lines* are the regression line and the *shaded lines* represent the 95% confidence interval

diverging trends of temperature and precipitation might have significant impacts on plant growth and forest productivity, given that the rapidly increasing maximum temperature enhances evapotranspiration and will negatively impact soil moisture availability in the drier spring season (Schickhoff et al. 2015). The increasing rainfall at Lete and almost stable rainfall at Thakmarpha is contrary to the enhanced frequency of winter and pre-monsoon drought reported from western Nepal (Wang et al. 2013). While the climatic trend of the Trans-Himalayan region (Mustang) showed the typical regional pattern of a rapid increase in maximum temperature and almost stable trend in minimum
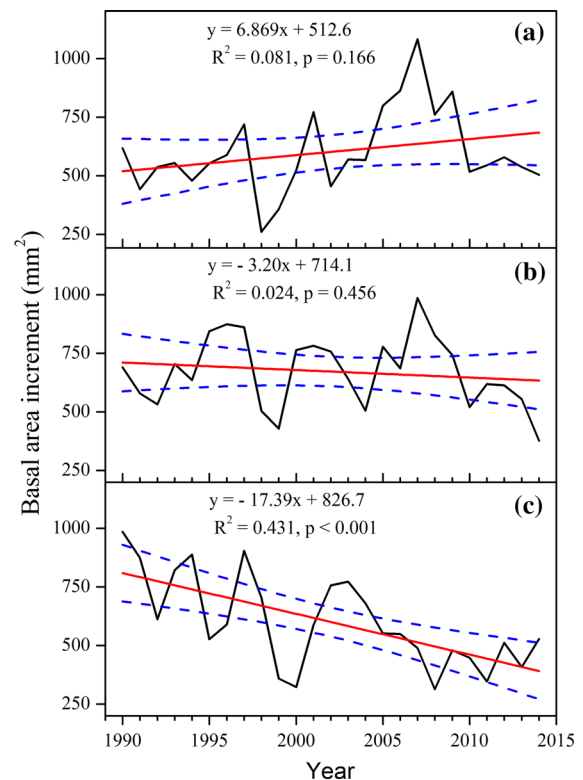
temperature, local precipitation trends show more variability. A consistent trend of increasing average rainfall was reported in the central Himalayas except the Northern Triangle temperate forest ecoregion (Shrestha et al. 2012), irrespective of decreasing precipitation trends in Western Himalayas (Kumar and Jain 2009). This contrast limits broad generalizations of climate trends and vegetation responses in the region (Schickhoff 2005; Miehe et al. 2015; Tiwari et al. 2016). We emphasize that the climate of the interior of the topographically complex Trans-Himalayan region is highly spatially variable and regionally complex so that extrapolation of future precipitation trends and forest responses for the region could be misleading.

Ring width chronology and growth–climate response

Our results demonstrated that the radial growth of *B. utilis* was mainly limited by temperature-induced

moisture stress during the spring season both at treeline (MT) and timberline (DT), irrespective of substantial differences in total rainfall between sites. The spring season rainfall and maximum temperature were relatively more important than mean temperature in the dry timberline site (DT). Our findings are in agreement with the moisture sensitivity of birch reported from the upper timberline in central Himalaya (Dawadi et al. 2013; Liang et al. 2014; Gaire et al. 2016), and for *Abies spectabilis* from the semi-arid treeline in the Trans-Himalayan zone (Tiwari et al. 2016). However, tree growth at high altitudes and latitudes was also reported to have been favored by high summer temperature (Barber et al. 2004; Chen et al. 2011). In our results, the temperature sensitivity of birch at MT was seen in the negative correlation with mean temperature (T_{mean}) of early spring (Feb–March), which was less strong at DT.

Our results revealed that spring season precipitation was more important for radial growth at DT in comparison with MT; this could be because of higher temperature and increased competition between trees at DT and also due to precipitation deficit in that area, in comparison to sparse trees and higher precipitation at MT, as has been reported in various studies in Himalaya and Tibet (Lv and Zhang 2012; Qi et al. 2015; Tiwari et al. 2016). Spring season climate is critical for *B. utilis* in the Himalayan highlands as shoot, leaf, and floral buds begin to sprout during April (Bisht et al. 2014), and warmer springs can contribute to elevated frost damage and reduced water availability, with consequent negative impacts on tree growth (Körner 2003). The early growing season (Feb–May) mean temperature (T_{mean}) sensitivity in the treeline sites could be associated with snow pack accumulation, as most of the precipitation during this time falls in the form of snow. The timing and duration of snow accumulation are important factors in the treeline where early warming (increase of T_{mean}) of growing season (Feb–March) could facilitate budding and shoot formation (Bisht et al. 2014) and radial growth by snow melt (Vaganov et al. 1999; Bekker 2005). However, there is a chance of heat-induced water deficit during the spring season and any such drought exposure could affect growth and seedling establishment at treelines, and may even cause retreating of treeline (Liang et al. 2014).

In this study, we reported more or less similar climate growth response at MT1, MT2, and DT, although the strength of the correlation differed. Tree radial growth showed a stronger negative response to maximum temperature (T_{max}) at DT (Fig. 5), implying that projected warming will negatively impact future growth as drought stress intensifies at DT, given consistent warming and low precipitation in the region (Figs. 1, 2, 3). In the Himalayan region, moisture stress during spring season (March–May) was found to limit the radial growth of *B. utilis* even at the treeline (Gaire et al. 2016). Some studies in the Himalaya also reported radial growth of *A. spectabilis* to be temperature sensitive (Bräuning 2004; Borgaonkar et al. 2011; Gaire et al. 2014), and they explained a negative relationship between spring climate and radial growth as threshold effects of moisture or temperature. Further, they emphasized heat-induced water deficit associated with high velocity of wind and increased evapotranspiration, to have negative influence on tree growth (Cook et al. 2003; Gaire et al. 2014). We infer that the precipitation seasonality is highly important for systems with a short growing season in higher altitude, with a shorter time for plants to compensate for a dry period, and especially so when the season is also characterized by high temperature (Spence et al. 2015). However, we also emphasize here that, although the rainfall is increasing in the moist region like Lete Lekh, and it is stable in the semi-arid region like Chimang, if precipitation is increasingly falling as rainfall rather than snow, soil water recharge from snow could further decline. Hence, even where overall precipitation is increased, the site might even be drier in the summer since water from rain flows away quickly, while the water from snowmelt seeps gradually into the soil over a longer period (Müller et al. 2016). Consequently, accurate characterisation of snow fall is desirable to help understand if weaker spring precipitation and continuous warming will drive further decline of birch radial growth and vitality in the semi-arid region of Mustang.

Temporal pattern of radial growth

In mature forest stands, age-related trends of BAI are generally positive. BAI may continue to increase in healthy stands (LeBlanc et al.1992; Duchesne et al. 2003), or stabilize (LeBlanc et al. 1992), but it does not show a decreasing trend until trees begin to senesce or

unless trees are subject to significant growth stress (LeBlanc et al. 1992; Weiner and Thomas 2001; Duchesne et al. 2003; Jump et al. 2006). Our results showed that the BAI of birch at MT1 and MT2 typically followed a sigmoidal pattern as it increased rapidly from young to middle age and remained almost stable during period of middle and older age as described by Spiecker et al. (1996) and Weiner and Thomas (2001). We report abruptly decreasing BAI of birch trees in the semi-arid timberline (DT) over recent decades in comparison to that of relatively moist treeline (MT). The negative influence of warm-day conditions (T_{max}) to radial growth also indicated that the semi-arid high mountain biota is experiencing temperature-induced drought stress (Fig. 5c, f). This finding emphasizes that tree growth and productivity in the semi-arid high mountains might further decline under the projected warming scenario (IPCC 2013). The contrasting growth trend of birch at moist treeline and semi-arid timberline sites showed the strong influence of precipitation associated with increasing warm-day conditions. The decrease of BAI at DT should be interpreted with some caution, however, because of lower canopy exposure at DT than MT, and potentially higher competition between trees in this semi-arid zone. In contrast, MT is characterized by comparatively less competition and a more open canopy (Spiecker et al. 1996), which might contribute to increasing/stable BAI at MT. Furthermore, nutrient availability, soil quality, and topographic exposure also play important roles in modifying local growth patterns of birch forests in the region (Müller et al. 2016). Nonetheless, given the growth–climate relationships identified, we believe that structural differences and potential-localized site quality variation between the treelines do not adequately explain BAI decline at DT, since this site would be expected to show lower BAI with lower individual tree resource availability but not declining BAI over time.

Consequently, we interpret our results as demonstrating that declining BAI at the semi-arid site is an early signal of growth decline at DT over the recent decades, due to increasing drought stress. Although growth climate analysis revealed DT to be more sensitive to precipitation than temperature, we emphasize that the increasing temperature in the future (IPCC 2013) would further intensify any temperature-induced drought stress in the region. *B. utilis* is an important early successional species in the Himalayan

treelines (Shrestha et al. 2007) and therefore a highly significant species in terms of forest ecosystems in the Himalayan highlands, declining growth in this species might alter competitive relationships, and hence, future forest composition at the lower range edge in the semi-arid forest of Chimang Lekh.

Conclusion

The spatial variability of climate in the interior of high mountain regions like the Himalayas is high due to interactions of complex topography and rain shadow effects. Although climate warming is generally expected to have an ameliorating influence on plant growth at high elevation, leading to upward elevational shifts of tree species, the positive influence of increasing temperature is not always universal in such regions. Strong gradients of precipitation over short distances result in high-altitude forests showing varying sensitivity to temperature and moisture. We find that spring precipitation and temperature are critical for radial growth of Himalayan birch, yet precipitation is more important than temperature at drier sites. Birch radial growth declined significantly at the dry site investigated here, where the rainfall trend is almost stable despite increasing temperatures over the recent decades. No such growth decline is seen in the wet site, where moisture availability remains adequate. Decreasing birch radial growth at its lower range edge demonstrates the negative influence of increasing temperatures in contrast with the moist upper treeline. Our results highlight the strongly spatially variable response of Himalayan birch to elevated temperatures and changing precipitation patterns in the region and can refine our understanding of likely responses of mountain forests to climate change.

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